INBREEDING IN MAN

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INTRODUCTION

In investigations on human populations from the point of view of heredity a primary assumption generally is that of random crossing, that is *panmixie*. Undoubtedly in many cases this assumption is sufficiently accurate. Various problems concerning the hereditary composition of populations previously have been treated on this basis by the present author (DAHLBERG 1926, HULTKRANTZ and DAHLBERG 1927).

However, *panmixie* does not always prevail. Deviations from the results that would arise from random crossing, may be caused in several ways. First, deviations may be caused by *selection*. Hereditarily differing individuals, may differ in their rate of reproduction. The effect of selection in regard to heredity, has been treated from a mathematical point of view in the works just quoted and by several other authors. Especially thorough are HALDANE'S works. Another cause of departure from *panmixie* is the existence of *isolating and mixing processes* within a population. This problem has been treated in a recent paper by WAHLUND 1928.

A third cause of deviation from the conditions at random crossing, is *consanguineous marriage*. Other causes of deviation might be conceived. Character bearers of a certain kind may marry each other with particular frequency, and so forth. In practice however, the three causes mentioned surely are the most important. The purpose of the present work is to investigate consanguineous marriage in man from the hereditary point of view.

The effects of inbreeding of animals and plants, have been mathematically treated by several authors. (Compare H. FEDERLEY, 1927. This

work gives an exhaustive list of authors). One has started with a cross of a certain kind, for example, between two heterozygotes and then proceeded on the assumption of an extreme of inbreeding, self-fertilization, crossing between sibs etc. In some works, also, selection has been assumed, prevention of reproduction of non-desirable character bearers, as a rule recessive homozygotes, etc. In human populations conditions differ in all these respects. Consanguineous marriage in man is of more accidental character, never reaches such extreme degrees, and is not always combined with systematic selection. No thorough theoretical inquiry into the effects on consanguineous marriage in man exists, though, of course, certain conclusions have been drawn from analogous conditions in the animal and vegetable realms. In principle, obviously, the chances of homozygosity arising through the coincidence of recessive genes, are increased through marriage between relatives, consequently the frequency of recessive character bearers is increased by these marriages. But so far we have had no measure for the strength of this influence, that is, the effect of marriage between relatives, and consequently no measure for the relative importance under given conditions of different kinds of consanguineous marriage. Obviously marriage between close relatives heightens the chances for homozygosity more than does marriage between individuals more distantly related. But having no conception of the degree of influence exerted by inbreeding, one has not been able to draw the line between the kinds of consanguineous marriage that have any practical importance, and the kinds that may under certain conditions be expected to have no appreciable importance, and so may be left out of account. The limits of what is to be considered as consanguineous marriage also are very differently placed by different authors, which, under these conditions, is not surprising. My present object is to get some more definite measure for the degree of influence that from different points of view is to be ascribed to consanguineous marriage.

With a view to the methods of research in regard to heredity in man, LENZ (1919) has calculated the frequency of consanguineous marriage that is to be expected among the parents of recessive character bearers at greater or less frequency of character bearers in the population. This work has proved very important in regard to methods of genetic research. Consanguineous marriage, however, may be of importance in yet other respects.

In regard to heredity a human population may be viewed from the following aspects:

1. The population may be taken as a whole, the object being to find

how far a certain frequency of consanguineous marriage changes the composition of the population as compared with *panmixie*.

2. One character bearer may be taken as the starting-point, and his nearest surroundings in the population examined, the object being to find how far a certain frequency of consanguineous marriage changes the hereditary qualities of his relations as compared with *panmixie* (and how often consanguineous marriage occurs among his parents—see above).

3. An individual may be taken, assuming among his relatives a certain number of character bearers, a certain number of non-character bearers, and a certain number of relatives of unknown quality, the object being to find what risk he runs, if marrying a non-relative, of his children being character bearers, and further what the risk is in the case of his marrying a relative.

These problems will be treated for the most part under the assumption of mono-hybrid inheritance.

EFFECTS OF CONSANGUINEOUS MARRIAGE ON A POPULATION

In drawing up formulas for the occurrence of heterozygotes and recessive, or dominant homozygotes for a simple Mendelian character in a population, the nature of the gametes may conveniently be used as starting-point. Assume that a recessive factor, R, occurs with a frequency of r in a population, and that the corresponding dominant factor, D, occurs in the gametes of the population with a frequency of d, obviously in that case $r+d=1$. Under the assumption that the $R-$ and $D-$ gametes are fortuitously brought together, the three different combinations of zygotes must have the following frequencies:

Recessive homozygotes (RR)..... r^2
Heterozygotes (RD)..... $2rd$
Dominant homozygotes (DD)..... d^2

These expressions make possible a calculation of the composition of a population when the proportion of recessive or dominant character bearers in a population is known. Concerning these conditions, see further the above-mentioned work by HULTKRANTZ and DAHLBERG (1927).

The above formulas, however, postulate random mating. This implies that a certain amount of inbreeding will occur. Theoretically the assumption is that marriage may be entered even between brother and sister, and between parent and child. In reality, of course, these crossings practically never occur. Other consanguineous marriages, for example marriage between cousins, on the other hand, possibly are commoner than

would be the case if the individuals of the population met purely by chance. *A priori* it is known that consanguineous marriage tends to increase the number of homozygotes and to reduce the number of heterozygotes, consequently, from the point of view of the character bearers, to increase the number of recessive character bearers, and reduce the number of dominant ones. Thus non-occurrence of marriages between brother and sister and parent and child, causes a reduction of the number of recessive character bearers. An over-representation of other consanguineous marriages, on the contrary, would entail an increase of the number of recessive character bearers. These two factors, therefore, to a certain extent cancel each other. In order to gain an understanding of the effects in this respect, it is necessary first to have an idea, how often random consanguineous marriage ought to occur. Then we shall have to form a conception of the actual frequency of consanguineous marriage, and to get a measure for the different kinds of effects of such marriages, and finally to attempt a conclusion from these data.

The frequency of chance consanguineous marriages

As families and other kinds of relationship exist within a population, consanguineous marriage must with greater or less frequency occur, if it is assumed that marriages are concluded at random. Our first object is to form a conception as to the frequency of the different degrees of consanguineous marriage under that condition.

Assume that the population consists of a number of individuals $= n$, and that the average number of children per marriage is $= c$. Here naturally, only the individuals that marry have to be counted, as the object is to calculate the marriage frequency. Taking a chance individual from the population, he has $c-1):2$ sibs which he might marry. The individual, of course, can only marry a sib of opposite sex, and we assume the same number of male and female individuals in the population. The whole number of individuals which he might marry is $n-1):2$, and the probability of his marrying a sib under these conditions is

$$\frac{c-1}{n-1}.$$

It will be seen that the difference of sex can be left out of account. Sex difference acts as a selective moment, preventing marriage in the case of relatives as well as regarding individuals in the population at large, and therefore can be neglected.

The probability of marriage between children and parents is calculated

under the assumption that the parent generation consists of a number of individuals $= n_1$. If the number of children $= c$, is unchanged from generation to generation, the number of individuals in the children's generation will be $\frac{n_1 c}{2}$ and consequently

$$n + \frac{n_1 c}{2} = n.$$

Thus $$n_1 = \frac{2n}{2+c}.$$

The parents' generation therefore is $\frac{2}{2+c}$ of the whole population, and the children's generation $\frac{c}{2+c}$ of the population.

Thus taking a chance individual from the population, the probability of his belonging to the parents' generation is $\frac{2}{2+c}$ and the probability of his marrying one of his children is $\frac{c}{n-1}$. However, the possibility also has to be reckoned with that he belongs to the children's generation, and that he marries an individual from the parent's generation. The probability of marriage between children and parents therefore must be doubled, or

$$2 \cdot \frac{2c}{(2+c)(n-1)}.$$

The probability of marriage between parents' sibs and children is calculated in the same way. The probability of an individual belonging to the parents' generation is $\frac{2}{2+c}$ The individual has $(c-1)$ sibs, and consequently $c(c-1)$ sibs' children, thus the probability of marriage between parents' sibs and sibs' children is

$$2 \cdot \frac{2c(c-1)}{(2+c)(n-1)}.$$

Obviously, in this case also, the double possibility must be reckoned with, that of the individual belonging to the older generation and marrying one of the younger generation, and that of the individual belonging to the younger generation and marrying one of the older.

The probability of marriage between cousins, finally, is calculated in the following way. A chance individual has $2c(c-1)$ cousins. The total number of individuals which he can marry is $(n-1)$. Therefore the probability of marriage between cousins is

$$\frac{2c(c-1)}{n-1}.$$

The probability of other consanguineous marriages is calculated in the same way. Thus the probability of marriage between cousins and cousins' children is

$$2\cdot\frac{4c^2(c-1)}{(2+c)(n-1)}.$$

The probability of marriage between cousins' children is

$$\frac{4c^2(c-1)}{(n-1)}.$$

The general formula for marriages between relatives belonging to the same generation is

$$\frac{2^g c^g (c-1)}{(n-1)}$$

where the number of children $= c$, the number of individuals in the population $= n$, and the number of generations between the relatives and the common ancestors $= g$, not counting the ancestors and their own generation. The general formula for the frequency of marriages between relatives separated by one generation (except between parents and children, see above), is

$$2\cdot\frac{2^g c^g (c-1)}{(c+2)(n-1)}.$$

where the number of generations separating the last generation from the common ancestors $= g$, not counting their own generation and that of the ancestors.

The formulas show that the further consanguinity is counted, the more frequent consanguineous marriages become, the consequence being that taking consanguinity in a sufficiently wide sense, all marriages may be regarded as consanguineous. The same conclusion of course results from considerations as to the number of ancestors of an individual, because otherwise this number, even counting a very moderate number of genera-

tions, reaches impossible values. This conclusion may also be said to be implied in the evolution theory. Consequently *panmixie* necessarily must be the primary assumption, if a point for comparison of the effect of a certain degree of inbreeding is to be found. Obviously it is not possible to make comparisons with a population without inbreeding, as *au fond* all marriages are consanguineous.

The above formulas express the probability under schematic conditions (*age differences being left out*) of consanguineous marriage of differing degrees under the assumption of random crossing. A common characteristic of the formulas for the higher degrees of consanguinity, is that when the number of children compared to the population is very small, the probability of chance consanguineous marriages approaches zero. However, in the case of a limited population the figures are not so low that they can be *a priori* omitted. Figures for the frequency of some different kinds of consanguineous marriage at varying size of population, and under the assumption that the children reaching marriageable age and marrying, are two or three per family, are given in table 1.

TABLE 1

Calculated frequency of consanguineous marriages at panmixie and rising population and with two and three children, respectively, per marriage.

SIZE OF THE POPULATION	SIB MARRIAGES PERCENT		PARENTS×CHILDREN PERCENT		PARENTS' SIBS×SIBS' CHILDREN PERCENT		COUSIN MARRIAGES PERCENT	
	2 Children	3 Children	2 Children	3 Children	2 Children	3 Children	2 Children	3 Children
50	2	4	4	4.8	4	9.6	8	24
100	1	2	2	2.4	2	4.8	4	12
300	0.33	0.66	0.66	0.8	0.66	1.6	1.33	4
500	0.2	0.4	0.4	0.48	0.4	0.96	0.8	2.4
1,000	0.1	0.2	0.2	0.24	0.2	0.48	0.4	1.2
5,000	0.02	0.04	0.04	0.048	0.04	0.096	0.08	0.24
10,000	0.01	0.02	0.02	0.024	0.02	0.048	0.04	0.12
100,000	0.001	0.002	0.002	0.0024	0.002	0.0048	0.004	0.012
1 000,000	0.0001	0.0002	0.0002	0.00024	0.0002	0.00048	0.0004	0.0012

From this table it appears that if, for instance, the number of children per marriage is 2, and the population numbers 500, the frequency of chance marriages between sibs is 0.2 percent, that of marriage between parents and children and of marriage between parents' sibs and sibs' children 0.4 percent, and of marriage between cousins 0.8 percent. If on the other hand, the population is put at 10,000, and the number of children

at 3, the corresponding figures are, for sibs 0.02 percent, for parents and children 0.024 percent, for parents' sibs and sibs' children 0.048 percent, and for cousins 0.12 percent. These figures prove that when the population is not of very considerable size, under *panmixie* consanguineous marriages have to be reckoned with in percentages that are not quite insignificant. In principle these conclusions should not be invalidated by our not having taken the age of the individuals into account. It will be evident from our formulas that the frequency of consanguineous marriage in a population under otherwise equal conditions, depends on the average size of the families.

Empirical occurrence of consanguineous marriage

Proceeding to a review of the available data as to the actual occurrence of consanguineous marriage in different populations, our intention is not to give an exhaustive survey of the existing statistics, only to obtain a moderately secure basis for our calculations.

In the offical statistics of some countries figures are given for the frequency of consanguineous marriages of different kinds. Some data will be found in table 2.

TABLE 2

Frequency of consanguineous marriages in France, Bavaria, and Prussia.

COUNTRY	NUMBER OF CONLUDED MARRIAGES	MARRIAGES BETWEEN PARENTS' SIBS AND SIBS' CHILDREN		COUSIN MARRIAGES	
		Number	Percent	Number	Percent
France					
1876–1900	7086567	5121	0.072	67587	0.95
1901–1910	3047183	1629	0.054	26404	0.87
Bavaria					
1879–1899	811277	584	0.072	4710	0.58
Prussia					
1875–1899	5922439	3546	0.060	34762	0.59

It will be seen from these figures that the frequency of marriage between cousins, varies between 0.5 and 1 percent, and that of marriage between sibs' children and parents' sibs keeps under 0.075 percent. LENZ 1919, puts the frequency of consanguineous marriage at the following percentages: parents' sibs × sibs' children 0.06 percent, cousins × cousins 1 percent, cousins × cousins' children 0.3 percent, cousins' children × cousins' children 1 percent. WULZ (1925) has examined 42 parishes in an area northwest of

Munich for the years 1848–1922, and his figures are in fair accordance with those from Bavaria (marriage between cousins 0.6 percent, parents' sibs×sibs' children 0.01 percent on 16,182 marriages). SPINDLER (1922) has examined the frequency of consanguineous marriage in three Würtemburgian villages. Among 453 marriages he found no marriage between parents' sibs and sibs' children. Marriages between cousins were 1.8 ± 0.8 percent, between cousins and cousins' children 0.7 ± 0.4 percent, and between cousins' children 7.1 ± 1.2 percent. REUTLINGER (1922) gives some figures for consanguineous marriage among Jews in Hohenzollern. Eighty-two out of 117 marriages were in a town of 1320, and 35 in a town of 4320 inhabitants. The frequency of marriage between cousins was 16.2 percent and between cousins' children 2.6 percent. REUTLINGER got the information by questioning the parties, and it is comparatively uncertain for the more distant relationship.

These figures confirm the conclusions from our above formulas, namely that the frequency of consanguineous marriage is higher in small populations than in large. Judging from the empirical figures, it seems the frequency of marriage between cousins can be put at the figure propounded by LENZ, or 1 percent, and that of marriage between parents' sibs and sibs' children at 0.7 percent (a little higher than the figure proposed by LENZ). Naturally these figures, that refer in the first place to West European official statistics, can have no pretence to universal validity. Obviously conditions vary in different populations. In the absence of more thoroughgoing statistical investigations, however, it would seem to be justified taking these figures as basis for our calculations.

Hereditary constitution of offspring in consanguineous marriages

The following calculations are based on the formulas for composition of the population reproduced on p. 423. We assume that a recessive character has the probability r, and that consequently, a recessive character bearer has the probability r^2.

First the probable constitution of the offspring in a marriage between children and parents will be calculated. Taking a chance marriage of this kind, and one of the parent's genes, also fortuitously chosen, this gene has the probability r of being *R*. What, then, is the probability of this gene meeting with itself in homozygous form in the descendants? The probability of the gene in question being transmitted directly from one of the parents to the offspring is 1/2 (figure 1). The probability of its reaching one of the children assumed to marry one of the parents, also is 1/2, and

the probability of its being transmitted from this child to the offspring, once again 1/2, consequently the final probability $1/2 \cdot 1/2 = 1/4$. The probability of a gene meeting itself, that is passing both directly and via one of the children, consequently is $1/2 \cdot 1/4 = 1/8$.

However, we have to reckon with 4 genes in the parents, any one of which may occasion this conjunction. Thus the probability is quadrupled; the probability of a conjunction therefore is $4.1/8 = 1/2$. The probability of the original gene being a carrier of the recessive character is r. There-

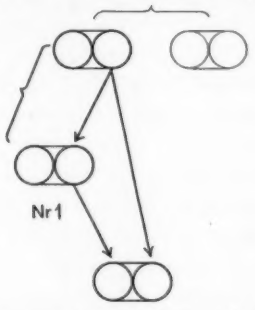

FIGURE 1.—Marriage between parent and child; the pairs of genes represented by joined circles

fore, the probability of a gene meeting itself in the offspring, producing a recessive character bearer, is 1/2r. In the other 1/2 cases, when a gene does not meet itself, but combines with a gene deriving from different original genes, recessive character bearers should result with the same frequency as at random meeting of genes in the population, that is in r^2 cases. Thus, in half the cases character bearers would result in r^2 cases, that is with the probability $1/2r^2$, and the probability for character bearers among the offspring in a marriage between children and parents would be

$$\frac{1}{2}r + \frac{1}{2}r^2.$$

In order to calculate the probability for the constitution of the offspring in a marriage between sibs, take a gene in one of the parents (figure 2). The probability of this gene passing to one of the children is 1/2, and of its passing to their children 1/4. The probability of its meeting there with itself is $1/4 \cdot 1/4 = 1/16$. Here also, however, we have to reckon with 4 original genes; the probability of any of those being a carrier of the recessive character is r. Thus, the probability of a recessive gene meeting itself in the grandchildren, and constituting a recessive character bearer, is

$4r \cdot 1/16 = 1/4r$. In the other 3/4 cases character bearers can be produced by R genes descended from different original genes meeting in RR combinations. This happens in r^2 cases, as the proportion of R genes in the original individuals must be the same as in the population at large $= r$. The

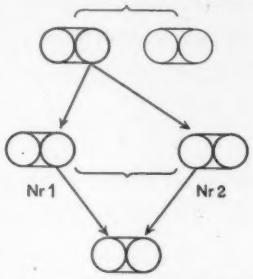

FIGURE 2.—Marriage between sibs (see FIGURE 1).

probability for recessive character bearers in the offspring of a marriage betwee sibs consequently is

$$\frac{1}{4}r + \frac{3}{4}r^2.$$

Calculating the probability for character bearers in the offspring of a marriage between parents' sibs and sibs' children, we proceed from the

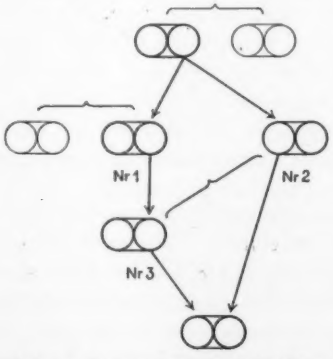

FIGURE 3.—Marriage between parents' sibs and sibs' children (see FIGURE 1).

parents of the "parents' sibs" (figure 3). A gene in one of these has the probability 1/2 of recurring in one of the "parents' sibs," and 1/4 of recurring in one of their children. The same gene has a chance of 1/2 of reaching the parents' sibs, 1/4 of reaching the sibs' children, and 1/8 of

reaching their offspring. The probability of a gene meeting itself in the offspring thus is $1/8 \cdot 1/4$. As usual we have 4r possibilities of the gene being a character carrier. Taking into account the character bearers produced by the coincidence of genes that are carriers of the character, but are descended from different original genes, the probability for recessive character bearers among descendants from a marriage between parents' sibs and sibs' children is

$$\frac{1}{8}r+\frac{7}{8}r^2.$$

Finally, the constitution of the offspring of a marriage between cousins is to be calculated (figure 4). An original gene has the chance 1/2 of reach-

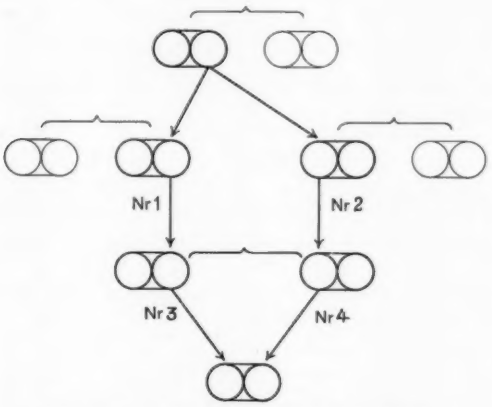

FIGURE 4.—Marriage between cousins (see FIGURE 1).

ing the children, 1/4 of reaching the grandchildren, that is the cousins, and 1/8 of reaching their children. The probability of its coinciding with itself in these, consequently is $1/8 \cdot 1/8$. As there are 4 original genes, the probability of a gene coinciding with itself is 1/16. The probability that a gene meeting with itself is a character carrier, is the same as in the population at large, that is r, consequently character bearers are produced by the coincidence of R genes originating from the same original gene in 1/16r cases. In the other 15/16 character bearers are produced by the chance coincidence of genes descended from different original genes (naturally not only from the common grand-grandparents). This must occur with the same frequency as in the population at large, that is in r^2 cases, and the

final result is that the probability for recessive character bearers among the children of a marriage between cousins is

$$\frac{1}{16}r+\frac{15}{16}r^2.$$

Similarly it can be calculated that the probability for recessive character bearers among the offspring of marriages between cousins and cousins' children is

$$\frac{1}{32}r+\frac{31}{32}r^2,$$

and further that the probability for recessive character bearers among the offspring of marriages between cousins' children is

$$\frac{1}{64}r+\frac{63}{64}r^2.$$

An examination of these formulas will show that the general expression for the frequency of character bearers among the offspring of consanguineous marriage is

$$\frac{1}{2^s}r+\frac{2^s-1}{2^s}r^2$$

where r = the frequency of the recessive gene in a population, and s = the number of intermediary stations passed by the gene between ancestor and descendant. Consequently, in a marriage between parents and children s = 1, in a marriage between sibs s = 2, between parents' sibs and sibs' children s = 3. The number of intermediary stations, that is individuals through which the gene has to pass before meeting itself, is clearly seen in the figures appended to our calculations, in which these intermediary stations have been numbered.

Through this formula we have obtained a measure for the increase of homozygozity (frequency of *RR*-individuals), conditioned by different classes of consanguineous marriage. Obviously the dominant character bearers (*DD*- and *DR*-individuals) decrease to the same extent that the recessive character bearers increase. The increase of dominant homozygotes (*DD*-individuals) can be obtained by inserting the frequency of the dominant gene in the formula. By adding the increase of recessive to that of the dominant homozygotes, the decrease of heterozygotes is obtained.

It should however be remembered that although the number of homozygotes is increased, and that of heterozygotes reduced through consanguineous marriages, the gene proportions are not changed. Consanguineous marriage only sorts together genes of the same kind to a greater extent than does *panmixie*, but does not change the percentage of genes in the population. Consequently, if the inbreeding ceases, the composition of the population is restored to the state that is to be expected at *panmixie*. Consanguineous marriages affect only the offspring of the related individuals marrying. If the children marry into the population, the effect of the consanguineous marriage is cancelled, but if in their turn they enter a consanguineous marriage, the effect is somewhat increased, because the parties to such a marriage are related in several ways, and the genes have several paths by which to meet with themselves. Such marriages, however, must be comparatively rare, and we do not propose to give the formulas' for these more complicated forms of consanguineous marriage. If will be understood from the above that completed consanguineous marriages in earlier generations have no influence. Consanguinity affects only the direct descendants—that is only that point in the population above which the consanguineous marriage takes place.

Conclusions

We have now the premises for an investigation of the effect of inbreeding on the composition of a population.

It has been shown above that the fortuitous occurrence of consanguineous marriage is infinitesimal if the population is very large, for example rising to millions. In that case, consequently, only the positive effect of actually occurring consanguineous marriages need be taken into account. Assuming that marriages between parents' sibs and sibs' children occur with the frequency $= P_3$, and marriage between cousins with the frequency $= P_4$, the population will have normal composition in $(1-P_3-P_4)$ percent cases, in P_3 cases the composition expressed by the formula for children of parents' sibs—sibs' children, and in P_4 cases the composition expressed by the formula for children of marriages between cousins. By adding these expressions, the composition of the population under the conditions assumed is obtained, and by subtracting r^2 the increase of the percentage of recessive character bearers compared with *panmixie* is obtained. Consequently the formula for increase is:

$$(1-P_3-P_4)r^2+\frac{P_3}{8}(r+7r^2)+\frac{P_4}{8}(r+15r^2)-r^2$$

or:

$$\frac{2P_3+P_4}{16}(r-r^2).$$

Employing the figures for empirical frequency of marriages between parents' sibs and sibs' children, given above, and considered as normal, we insert these in our formula. If the recessive factor has the frequency r, consequently the increase occasioned by these marriages is $0.07125(r-r^2)$. It will be seen from this expression as well as from the above general formula that the increase of recessive character bearers approaches 0, when the frequency of the factor approaches 0. The increase grows with r, reaching its maximum at $r=1/2$, then receding to 0 at $r=1$. The maximum increase at the frequencies assumed for consanguineous marriages is 0.0178 percent, that is so low as hardly to be statistically ascertainable. If higher figures for the frequency of consanguineous marriages are inserted, naturally we get a higher value for the increase. Even if the percentages for the two kinds of consanguineous marriage referred to, are multiplied by ten, the absolute increase, however, will be only 0.178 percent or almost negligible. Besides, it should be remembered that then r has been put at 1/2, which means that we get a maximal increase. In a case of a rare character, naturally the increase is still more insignificant. In order to demonstrate this circumstance, in the appended table 3 the increase in

TABLE 3

Table of the increase of the percentage of recessive character bearers at rising frequency of a monohybride factor in a popularion with only cousin marriages.

PERCENTAGE FREQUENCY OF A HEREDITARY FACTOR IN THE POPULATION	PERCENTAGE FREQUENCY OF RECESSIVE CHARACTER BEARERS IN THE POPULATION	PERCENTAGE INCREASE OF RECESSIVE CHARACTER BEARERS IN THE POPULATION
1	0.01	0.0619
10	1	0.562
20	4	1.00
30	9	1.313
40	16	1.50
50	25	1.562
60	36	1.50
70	49	1.313
80	64	1.0
90	81	0.562

the percentage of recessive character bearers is given for a population where all marriages are between cousins. Figures are given for the increase at different frequencies of the recessive character, and the corresponding

percentages for recessive bearers at *panmixie* are also given. By adding the percentage for character bearers at *panmixie* to the corresponding percentage for the increase, the percentage of recessive character bearers in a population where all marriages are between cousins, is obtained. The increase is calculated from the formula for marriages between cousins p. 426 and consequently is obtained by subtracting r^2 from $r/16+15r^2/16$. Thus

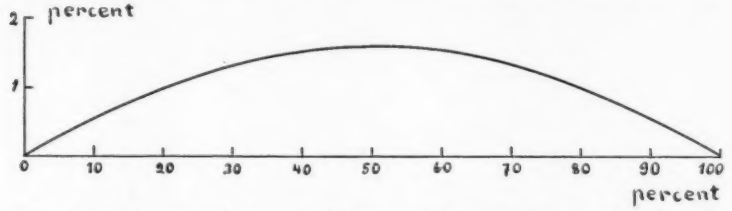

FIGURE 5.—Diagram of the percentual increase of character bearers in a population with only cousin marriages, compared to *panmixie*, at rising frequency of the factor. The vertical scale has had to be made 10 times as large as the horizontal one in order to make the curve perceptible.

the formula for the increase is $1/16(r-r^2)$. In order to obtain from this table for instance the increase at a percentage of 10 for marriages between cousins, the figures for the increase in this table are divided by 10, the increase at a percentage of 1 is obtained by dividing by 100. The increase in a population where all marriages are between cousins also is demon-

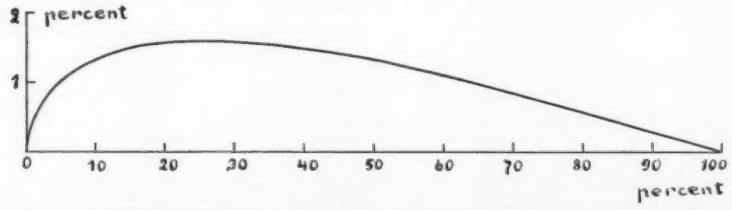

FIGURE 6.—Diagram of the percentual increase of monohybrid, recessive character bearers in a population with only cousin marriages, compared to *panmixie*, at rising frequency of character bearers. The vertical scale has had to be made 10 times as large as the horizontal one in order to make the curve perceptible.

strated by two diagrams (figures 5 and 6). Keeping in mind what may be regarded as reasonable frequencies and degrees of consanguineous marriage in human populations, a contemplation of the table and the diagrams will show, better than words, that in human populations the increase of recessive character bearers on account of consanguineous marriages never can be of any real importance.

As the increase at consanguineous marriages in more distant degrees of relationship is very much less evident there is no reason to carry out the demonstration for these degrees of relationship.

I wish to stress, that when, as here, it is said that consanguineous marriage is of no consequence, this is done in a statistical sense only. The increase of the number of recessive character bearers that may be caused by consanguineous marriage, can hardly reach such proportions as to be of any account statistically. But this does not mean that if the population is fairly large, the number of character bearers that can be assigned to this increase, may not be quite considerable. In the case of a country with several millions of inhabitants, a certain degree of inbreeding may cause a slight increase of the number of certain recessive character bearers, in comparison to a country with a lower frequency of inbreeding. Although this increase may not be observable with statistical methods, it may reach an amount of several hundred individuals. Insignificant though this figure may be relatively to the population as a whole, these individuals, however, may mean much suffering for the diseased and their families, and considerable expense for the community.

The above argument, however, applies only for very large populations. It is not to be precluded that counting smaller populations and taking into account the non-occurrence of marriage between sibs and between parents and children, we might find a negative effect, an increase of the heterozygotes occasioned by the reduced number of consanguineous marriages compared to *panmixie*. Therefore we proceed to examine the conditions for small populations, employing our formulas for the frequency of consanguineous marriages. Provisionally the non-occurring fortuitous frequency of marriage between sibs, will be $=p_1$; that of marriage between parents and children $=p_2$, between parents' sibs and sibs' children $=p_3$, and between cousins $=p_4$. Further the empirical frequency of marriages between parents' sibs and sibs' children $=P_3$, and the empirical frequency of marriages between cousins $=P_4$. The formula for the increase of recessive character bearers in the population in this case is:

$$(1-P_3-P_4+p_3+p_4)r^2+\frac{P_3-p_3}{8}(r+7r^2)+\frac{P_4-p_4}{16}(r+15r^2)$$
$$-\left[\frac{p_1}{2}(r+r^2)-p_1r^2\right]-\left[\frac{p_2}{4}(r+3r^2)-p_2r^2\right]-r^2;$$

This gives

$$\frac{2P_3+P_4-(8p_1+4p_2+2p_3+p_4)}{16}(r-r^2)$$

which expressed in c = number of children, and n = population, gives

$$2P_3+P_4-\frac{2c^3+18c^2+12c-16}{(2-c)(n-1)}(r-r^2);$$

This expression is 0—that is, consanguineous marriage is without effect, if

$$2P_3+P_4=8p_1+4p_2+2p_3+p_4$$

or

$$2P_3+P_4=\frac{2c^3+18c^2+12c-16}{(2+c)(n-1)};$$

Taking a given, empirical consanguineous marriage, and assuming a certain average number of children, we are thus able to calculate the size of population at which the effect of consanguineous marriage is none. If the population exceeds the calculated size for equilibrium, the result is an increase of homozygoty, that is of recessive character bearers. Even in the most favorable case, that is when the population is infinitely large, this increase is however, as demonstrated above, quite infinitesimal.

However, the point for equilibrium as calculated by the formula, must be higher than in reality, as, in working out the formula, it has been assumed that the age difference actually obtaining between parents and children, would not act as a check. As a matter of fact this age difference, even under the conditions of random crossing naturally must entail that the chances for such marriages become considerably less than indicated by the formulas. Employing the above formula, therefore, we reach an upper limit for equilibrium; the value obtained is too high. Assuming "normal" frequency of consanguineous marriage, and two as the number of children, we find that equilibrium obtains at 2104 individuals, that is in a population of about 2000. This, consequently, is the upper limit for equilibrium.

Assuming, on the other hand, no fortuitous marriages at all between parents and children, or between parents' sibs and sibs' children, we get the following formula:

$$(1-P_3-P_4+p_4)r^2-\frac{P_3}{8}(r+7r^2)+\frac{P_4-p_4}{16}(r+15r^2)-\left[\frac{p_1}{2}(r+r^2)-p_1r^2\right]-r^2$$

which gives

$$\frac{2P_3+P_4-8p_1-p_4}{16}(r-r^2):$$

This expression is 0, if

$$2P_3+P_4=8p_1+p_4$$

or if

$$2P_3+P_4=\frac{2c^2+6c-8}{n-1};$$

This formula gives too low a value for equilibrium. Putting the number of children at two, we find that equilibrium lies at 1053 individuals, that is at a population of about 1000 individuals.

These calculations show that consanguineous marriage at "normal" frequency has no influence, that is it does not cause any departure from *panmixie* when the size of the population is something between 1000 and 2000 individuals. A given frequency of consanguineous marriage, thus corresponds to a certain size of population, at which this frequency of consanguineous marriage has no effect. On the other hand, of course a certain figure for population answers to a certain frequency of consanguineous marriage, which must be found at *panmixie*, and which is necessary if the number of character bearers is going to be that, demanded by the formulas for *panmixie*. A curious consequence is that if two populations of similar composition, and both with *panmixie*, are joined, and if the frequency of consanguineous marriage remains the same as in the original populations, the number of character bearers in the joined population at *panmixie* will be somewhat larger than the added number in both the original populations. Another peculiarity is that if a population consists of one family of sibs, the number of character bearers produced by marriages between sibs, will be the same as that produced by fortuitous mating in a population as large and consisting of several families of sibs.

What is the effect of consanguineous marriage if the population is considerably smaller than required for equilibirum? In that case there will be an increase of heterozygosity in the population, that is a reduction of the number of recessive character bearers as compared to *panmixie*. If the population numbers 500, and the number of children is 2, the reduction will be found to amount to 0.0572 percent at normal frequency of consanguineous marriage. If the population numbers 200, and the number of children is 2, the reduction is 0.1697 percent.

These figures are maximal, being calculated from the first formula (p. 423), which gives too high values, as the age difference is not taken into account, and under the presumption that $r=1/2$. If the character is more rare, naturally the reduction will be still smaller. Further we have been reckoning with "normal" frequency of consanguineous marriage, that is to say with a frequency that for small populations must be abnormally low.

All of which conduces to give a figure for the decrease of recessive character bearers which is decidedly too high, compared to the frequency at *panmixie*. Nevertheless the decrease is quite infinitesimal, even for small populations, so that in practice it can be omitted. Thus, it is undoubtedly legitimate to say that in the case of small populations as well as large ones, no appreciable influence on the frequency of recessive character bearers in human populations, is to be expected. If on a comparison of the frequency of mono-hybrid character bearers in two populations, distinct differences in that respect are to be observed, this difference, consequently, is not to be explained by any larger or smaller frequency of consanguineous marriage in the two populations. In order to get a perceivable difference between two populations through consanguineous marriage, frequencies and degrees of consanguinity will have to be assumed that go far above what is reasonable or possible in human populations.

It may seem unnecessary to carry out such detailed calculations on the frequency of chance consanguineous marriages, as in the above. These formulas, however, are of interest not only in regard to the effects of consanguineous marriage, because, taking a large population, we are not justified in assuming that marriages are concluded at random over the whole of the population. An individual at a certain point in the population can marry only among a certain number of individuals in his immediate environment, while his chances of marrying the greater part of the individuals in the population, are small or none, due to geographical, social, or other reasons. In other words, a population resolves itself into part populations, or isolates, and only within these, random mating can be presumed. Carrying the argument into extremes, one might say that such limits of the isolates never completely coincide for two persons. From a more practical point of view it can be said that a population is divided up into regions, smaller areas, and social strata within which random mating can with sufficient accuracy be assumed. Between the isolates, a greater or less mixture takes place, and thus sooner or later homogeneity between the different isolates is reached. When homogeneity is reached, these limits are no longer of any importance in regard to heredity. The theory for the isolates cannot be treated here. Only one aspect of the matter will be touched on, namely the question of the numerical size of the isolates. Above, formulas have been given, indicating the frequency of consanguineous marriage at a certain assumed number of children, and a certain size of the population. The formulas also can be employed to calculate the size of the population if the frequency of consanguineous marriages and the number of children is known. It may be pointed out that here the

question is only of children who reach marriageable age, and do marry. If this number is 2, the population must be constant. If, again, the number of children per marriage is 3, and other conditions are the same, one generation would give an increase of 50 percent, that is, far more than in reality is to be found in populations generally. Judging from the actual increase, the number of children in Western Europe is about 2, or little over 2, that is if only children who reach marriageable age, and do marry, are counted. Thus, an assumption of 2 children will give a fairly accurate figure for the population.

For our following calculations we employ the figures given above as normal for the frequency of consanguineous marriage, and which, in the first place, refer to conditions in Western Europe. In the above calculations, these figures were taken without any discussion as to whether they actually correspond to what would be expected on account of random mating in these populations, or whether they indicate that consanguineous marriage is more or less common than conditioned by *panmixie*. Taking this problem under discussion, we now use the formulas previously worked out for the chance occurrence of consanguineous marriage. Can it, then, be said that consanguineous marriages occur with the same frequency as required by our formulas? Decidedly not. The empirical figure for marriage between parents' sibs and sibs' children, is quite certainly too low. To begin with, we have not, on working out our formulas for the chance occurrence of such marriages, taken into account the considerable average age difference between these categories of individuals. This age difference, of course, must act as a strong restraint, so that actually such marriages are less frequent than indicated by the formulas. Further, the reputation of harmfulness appending to marriages between near relatives, should work in the same direction. But if this figure is too low, we get too high a figure for the population, when it is used to calculate the population. We assume a number of 2 children per marriage, and thus, employing the formula for marriages between parents' sibs and sibs' children p. 425 arrive at a figure for the population of 2957, that is about 3000 individuals. This, then, can be regarded as the upper limit for the isolates in the population in question. The formula now gives the size of the isolates for both sexes. Taking into account the sex difference, the result is that on an average a certain person has, in these populations, the chance of marrying one out of less than 1500 individuals.

As regards marriages between cousins, there is no strong average age difference asserting a restraining influence. It rather seems an individual would have a greater chance of marrying a cousin, than other individuals

of his environment in the population, as, on account of their relationship, he will see his cousins comparatively often. Apprehensions as to the harmfulness of consanguineous marriages, would hardly play any rôle in the case of marriages between cousins. Under these circumstances, the empirical figure for marriages between cousins, would be rather too high, and in any case, hardly too low, compared to the frequency at random mating. Assuming 1 percent of marriages between cousins, and 2 children, consequently the resultant population would be somewhat too low. The figure is 400. This means that the isolates in the population on an average hardly fall below 400 individuals, and that every individual has a chance of marrying one out of at least 200 individuals.

The limits arrived at for the size of the isolates, thus lie at 400 and 3000. We also know that the upper limit is decidedly too high, because, as far as the formula is concerned, it is conditioned by a frequency for marriages between parents' sibs and sibs' children that is clearly too low. There is also reason to suppose that the figure for marriages between cousins is too high, and thus has given too low a figure for the isolates. Evidently nothing can definitely be said in this respect, even though the calculations may give grounds for a supposition that the isolates have to be denoted by three, rather than by four figures. It is also obvious that the size of the isolates is subject to very large variations, not only within a population, but also from one country to another. The one extreme is the large city, with its floating mass population, the other extreme is the forest region with scattered small villages, in, for instance, northernmost Europe. Under these circumstances, the working out of a more exact figure does not seem to be called for. The aim of the above calculations has been only to give an approximate idea of the "normal" order of the size of the isolates and to indicate a method for estimating their size in investigations on populations. The size of the isolates is a factor which acquires practical interest, when it is wished to analyse processes of mixture and equalization in different populations. Regarding the theory for these processes, I refer to WAHLUND'S work.

With regard to the effects of consanguineous marriage in a population, it is possible to say, however, that numerically the isolates do not diverge very far from the figure at which consanguineous marriage can be calculated to have no influence whatever, that is the composition of the population is the same as would be reached by *panmixie*. For Western Europe this figure was something between 1000 and 2000. It rather seems probable that the figure for the isolates (which falls between 400 and 3000) is lower than the figure for equilibrium, but in any case the divergence is

not of an order to let any appreciable influence of consanguineous marriage be expected. This applies to the increase or decrease of recessive character bearers at mono-hybrid inheritance.

However, speculating on the favourable or unfavourable influence of consanguineous marriage on a population, we have in mind not only the influence on one mono-hybrid character, rather the sum of influences on all the mono- and poly-hybrid characters in a population. Assuming a certain number of equally frequent mono-hybrid characters, the effect, of course, is as many times greater, as this number denotes. When, however, the effect for one character is near zero, the total effect for the sum of the mono-hybrid characters almost certainly will be so small, as to be negligible. The same applies to the effect for poly-hybrid characters. In order to prove this, we assume a di-hybrid, recessive character, carrying the two dispositions R_1 and R_2 with the frequencies r_1 and r_2. Recessive character bearers of the form $R_1R_1R_2R_2$ then occur with the frequency $r_1^2r_2^2$. We assume that consanguineous marriage occasions a divergence in the frequency of $R_1R_1 = \delta_1$ and a divergence in the frequency of $R_2R_2 = \delta_2$. Under these conditions recessive character bearers on consanguineous marriage will occur with the frequency

$$(r_1^2+\delta_1)(r_2^2+\delta_2) = r_1^2r_2^2+r_1^2\delta_2+r_2^2\delta_1+\delta_1\delta_2 \cdot$$

In this expression δ_1 and δ_2 are very small. They denote the increase caused by consanguineous marriage for each combination of homozygous dispositions, and as has been shown above, this increase is so small that it can be neglected. Consequently the terms in the above expression into which these factors enter, also are very small. Thus it can be said that the increase for di-hybrid, and analogically for other poly-hybrid characters, on account of consanguineous marriage, is small or none. For these as well, consanguineous marriage has no effect at all compared to ***panmixie***, if the size of the population corresponds to the equilibrium calculated above. If however, the size of the population diverges from this equilibrium, the effect, of course, is somewhat stronger in the case of poly-hybrid[2]

[1] The increase for the gene combination $R_1R_1R_2R_2R_3R_3 \cdots R_nR_n$ is:

$$(r_1^2+\delta_1) \cdot (r_2^2+\delta_2) \cdot (r_3^2+\delta_3) \cdots (r_n^2+\delta_n)$$

where R_1, R_2, $R_3 \cdots R_n$ are the different genes, r_1, r_2, r_3, $\cdots$, r_n their frequencies, and δ_1 δ_2, δ_3, $\cdots$, δ_n the increase of homozygosity for each pair of factors, conditioned by consanguineous marriage, according to our formulas. If the factors have equal frequencies, that is $r_1 =$, $r_2 = r_3 =$, $\cdots = r_n$ the formula is

$$R_1R_1R_2R_2R_3R_3 \cdots R_nR_n = (r_1^2+\delta_1)^n$$

WEINBERG has given general formulas for the composition of offspring in consanguineous marriages with complicated polyhybridity—without, however, giving any comments on the formulas

or several kinds of mono-hybrid characters; roughly speaking the effect for a di-hybrid character is less than for two monohybrid characters with corresponding frequencies. As, however, the size of the isolates does not diverge from equilibrium to such an extent as to leave an appreciable effect of consanguineous marriage for a recessive character, it follows that even in regard to several mono-hybrid or poly-hybrid characters it can be said that there is no reason to expect any greater divergence in the composition of the population, caused by consanguineous marriage as compared to *panmixie*.

Hitherto attempts have very frequently been made to explain different frequencies of hereditary character bearers in different populations, different classes, etc., through a varying frequency of consanguineous marriage. From the above it will appear that these explanations are not satisfactory. Whatever the cause may be of a different frequency of character bearers in a certain case, it is impossible that this difference, if it is a significant one, should be the result of varying degrees of consanguineous marriage.

THE INFLUENCE OF CONSANGUINEOUS MARRIAGE ON RELATIVES OF CHARACTER BEARERS

In the works quoted above (DAHLBERG 1926, HULTKRANTZ and DAHLBERG 1927) the authors have laid stress on the importance of taking into account in heredity research the average composition of the population from which the material is derived. If it is attempted, for instance, to find the proportion of blue-eyed individuals among the sibs of blue-eyed, obviously other figures must be expected if the material is taken from Sweden, than if it comes from Italy. Formulas have been worked out, by the aid of which can be calculated the average frequency of character bearers among the sibs, parents, children, parents' sibs, cousins etc., of a character bearer, at varying occurrence of a certain mono-hybrid character in a population. The formulas show that when the character is very rare in a population, one approaches limits which, naturally, are different for different kinds of relationship. Among sibs of recessive character bearers this limit is 25 percent or 1/4. If the character occurs with a frequency of 0.1 percent, the

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and without employing them for calculating the importance of consanguineous marriage for populations or individuals (WEINBERG 1909). In a later work (WEINBERG 1928) he has given the same formulas worked out also for monohybridity, and in the same way as LENZ 1919 drawn the conclusions with regard to the occurrence of consanguineous marriage among the parents of character bearers. Other aspects of the problems concerning the effect of inbreeding, have not been touched.

percentage among the sibs will be 25.6. In other words in the case of a comparatively rare character the hereditary composition of the relatives changes very little if the composition of the population is changed to some degree. If the character is rare, below a certain limit, it does not much matter whether it is more or less rare. For other aspects of this question, see the work quoted above.

The formulas mentioned above have been worked out under the supposition of *panmixie*. Will the hereditary composition of the relatives be changed to any considerable degree, if some consanguineous marriages occurr in the population? This can at once be denied. In the above it has been shown that the proportion of character bearers in a population is not appreciably influenced by inbreeding. In other words, in the case of a common character, the majority of character bearers are descended from the marriages of which it can be said that they would occur under *panmixie*, while only an inconsiderable number are descended from consanguineous marriages. For more common characters, thus, the formulas apply with sufficient accuracy, even if a certain amount of consanguineous marriage occurs. In the case of more rare and mono-hybrid dominant characters the majority of character bearers are heterozygotes. These are not, either, descended from consanguineous marriages, and consanguineous marriage, therefore, has no influence in the case of rare characters and dominance. For rare characters and recessivity, on the other hand, the majority of character bearers will be descended from consanguineous marriages. Will this influence the composition of the relatives? Taking one character bearer, we know that both the parents have the character in heterozygous form. Their two other genes are derived from the population, whether it is a case of consanguineous marriage or not. As the character is rare, these other genes must be the dominant ones. In any case, we have a heterozygous marriage, and find the limit of 1/4 character bearers among the sibs of the character bearer, whether the parents are related or not. Among the parents' sibs, grandparents and so forth, even in the case of consanguineous marriages, we practically never find a recessive homozygote, or heterozygote. Thus, if the character is rare and in the case of recessive inheritance, consanguineous marriage does not influence the proportion of character bearers among the relatives. The same holds good for different forms of polyhybridity, recessive or dominant. Generally it can be said that for the proportion of character bearers among the relatives of character bearers, fortuitously chosen in a population, no regard need be had to consanguineous marriage occurring in the population, and that the formulas worked out on the assumption of full *panmixie*, can be employed.

Intimately connected with this problem is the question, how often consanguineous marriage is to be expected among the parents of recessive character bearers. As mentioned above, LENZ 1919, has treated this problem, and demonstrated that if a character is rare, there is to be expected a perceptibly larger percentage of consanguineous marriage among the parents of recessive character bearers than in the population, and that the rarer the character, the greater is the increase of consanguineous marriage. This also can be illustrated by aid of the formulas given above. If there are P_3 cases of marriage between parents' sibs and sibs' children, and P_4 cases of marriage between cousins, there will under *panmixie* be recessive character bearers in $(1-P_3-P_4)$ cases, and in these consanguineous marriages there will be $P_3/8(r+7r^2)+P_4/16(r+15r^2)$ recessive character bearers. The chances for a recessive character bearer belonging to a consanguineous marriage thus are

$$\frac{\frac{P_3}{8}(r+7r^2)+\frac{P_4}{16}(r+15r^2)}{(1-P_3-P_4)r^2+\frac{P_3}{8}(r+7r^2)+\frac{P_4}{16}(r+15r^2)} = \frac{\frac{P_3}{8}\left(\frac{1}{r}+7\right)+\frac{P_4}{16}\left(\frac{1}{r}+15\right)}{(1-P_3-P_4)+\frac{P_3}{8}\left(\frac{1}{r}+7\right)+\frac{P_4}{16}\left(\frac{1}{r}+15\right)}.$$

If in this expression r is very small, the two terms above the line will be very large, likewise the equal two terms below the line very large compared to the first term, which at all times is near 1. If r approaches 0, therefore, the expression approaches 1; this means that the rarer a character is, the greater chance of the individual being descended from a consanguineous marriage, which by the way, is self-evident. Assuming the extreme case that a factor is to be found only in one individual in a population, for instance as the consequence of a single mutation, naturally recessive character bearers can arise only through marriage between descendants of this individual, that is through consanguineous marriage. Thus, a higher frequence of inbreeding is necessarily to be found among the parents of rare recessive character bearers. It must not be forgotten, however, that such an increased frequency may be found, because the material has been obtained from the smallest isolates of a population. (To give an extreme instance: Jews, compared to the population within which they are living.)

Such an increase, naturally does not prove the existence of hereditary factors, but may be occasioned by a comparison of non-corresponding groups.

As was previously said, the absolute increase of the number of recessive character bearers caused by consanguineous marriage thus is very small. Nevertheless the majority of the few character bearers that are to be found in a population, will be descended from consanguineous marriages. *From the point of view of the population, consanguineous marriage has very little importance for the occurrence of recessive character bearers. From the point of view of the character bearers, on the other hand, it has great importance, in the case of recessivity, and if the character is rare.*

Analogically, what is the importance of consanguineous marriage in regard to dominant mono-hybrid characters? Is there reason to expect a greater amount of consanguineous marriage among the parents of bearers of a rare, dominant character? If the character is rare, the majority of the dominant character bearers are heterozygotes. As was pointed out above, these are not particularly frequently descended from consanguineous marriage: consanguineous marriage even counteracts the production of heterozygosity. As the question was of heterozygotes, there will be no increased number of consanguineous marriages among the parents. In di-hybrid dominant heredity when, in the case of a rare character, a character bearer has been produced by the coincidence of two genes from different allelomorphous pairs, an increase of the frequency of consanguineous marriage should be expected among the parents of the character bearers, in analogy to the conditions under mono-hybrid recessivity. This applies also in different forms of poly-hybrid inheritance.

THE RISKS OF INDIVIDUAL CONSANGUINEOUS MARRIAGES

In the above it has been attempted to analyze the importance of consanguineous marriage for a population as a whole, and for the relatives of fortuitously chosen character bearers in a population. We have found that in these respects it is of little importance with regard to the frequency of character bearers. From the public point of view the risks of consanguineous marriage are small.

This does not mean that the risks are of no importance to the private individual. This might be illustrated by an analogy. The fire risk in towns is of course increased if the number of wooden houses, relatively to brick houses, is increased. However, it may be that the frequency of wooden houses is too low, and from one town to another varies within such narrow limits, that on a calculation of the average fire risk for different

towns, it is not necessary to take the wooden houses into account. The increase conditioned by these may be so small that it does not play any part if the risk is calculated for the whole town, or for fortuitously chosen houses. Nevertheless, it is necessary in the individual case to take into account the increased risk that may be conditioned by the proximity of wooden houses.

Our case is similar. If consanguineous marriage is of small consequence for the population, it does not follow that it is indifferent for a certain individual whether he enters into a consanguineous marriage. By such a marriage he may considerably increase his risk of having character bearers among his descendants. On the other hand this risk is naturally lessened by a consanguineous marriage, if it is known that the individual is himself healthy, and has no character bearers among his relatives.

Thus taking a certain individual, who has a certain hereditary trait, we want to find what risk he runs of having character bearers among his offspring in a consanguineous marriage, compared to that risk in another marriage, that is the risk of a consanguineous marriage in comparison to a "normal" one. What, then, is to be regarded as a normal marriage? One possibility is to calculate the average risk for a marriage with a fortuitously chosen individual in the population. Other possibilities are to assume that the other party is himself free from the character, that further he has healthy parents, sibs, grandparents and so forth. In the practical case, however, it is hardly possible to say anything about the qualities of the party that a certain individual would marry, if he did not conclude an intended consanguineous marriage, and so it seems more proper to take a fortutiously chosen individual for comparison.

For the primary individual, also, there are an unlimited number of possibilities. He may himself be a character bearer, or have one or more character bearers among his nearer or more distant relatives. Further it can be assumed that one or more of his relatives are not character bearers, and that a number of the relatives are of unknown quality. Evidently space would not allow the working out of formulas even for the immediately discernible cases, and below calculations only for two cases of cousin marriage will be carried out. If wanted, it should not meet any difficulties to make analogous calculations for other cases that may awaken interest. When a question is asked about the risks of a certain marriage, these calculations and points of view, may acquire some practical interest.

If these calculations are to be given general form one must take into account that the character may have different frequencies in the population; a formula may then be worked out from which, through inserting

the frequency for a certain gene, a figure for the risk may be obtained. Such formulas, however, are of comparatively small practical interest, as generally it is desired to calculate the risk only for relatively rare diseases etc. General formulas of this kind are comparatively complicated, and therefore will not be given in this connection; here the risk will be calculated only on the assumption that the character in question is very infrequent in the population. (Formulas of this kind will be given in a paper appearing in Archiv für Rassen- und Gesellschafts-Biologie.) Such calculations are very much simpler, and make far less demands on time and space. Not even with this limitation, however, it is possible to give the calculations for all the cases of immediate interest.

If a recessive factor is rare in a population, naturally the character bearers as well as the latent character bearers, also are very rare. It can thus be assumed that practically the whole population consists of free homozygotes. If an individual is a character bearer, or has a smaller or

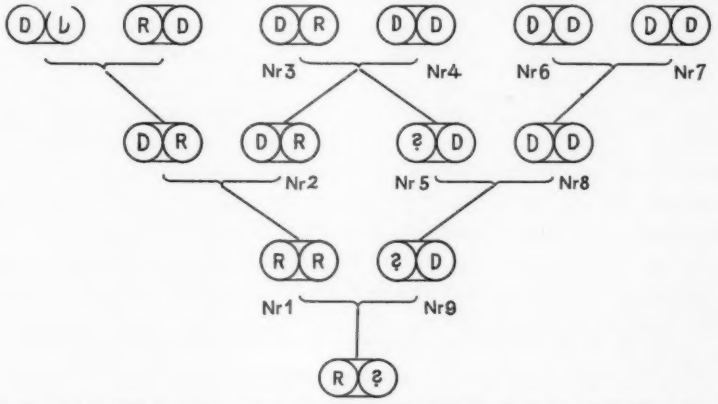

FIGURE 7.—Cousin marriage, one party having the recessive character, the other not, nor parents or grandparents.

greater number of character bearers in his family, he will in nearly every case, on a fortuitously concluded marriage to a non-relative, marry a healthy homozygote. The risk of a recessive character bearer among the children of such a marriage, is practically 0. It can thus be said that the normal risk in these cases is near 0.

If a person is a recessive character bearer, and concludes a marriage with a cousin, it is known with certainty that his parents are heterozygotes, and that the individual No. 2 in figure 7 has the composition RD. The

R-gene must also be found in one of the common grandparents; it has a probability of 1/2 to be found in No. 5, 1/4 to be found in No. 9, and 1/8 to be found in the children. In the cases where the R-gene is to be found in the children of No. 9, these children will be character bearers, because all the children receive an R-gene from No. 1. If the factor is rare, consequently the risk of recessive character bearers in a marriage between cousins is 1/8.

One more example will be given. Assume that one of the parents of the individual in question through whom he is related to the other party, is a recessive character bearer (see figure 8). In that case the individual with certainty is a heterozygote. Both the parents of the character bearer also are heterozygotes. Among their descendants 2/3 are heterozygotes, and

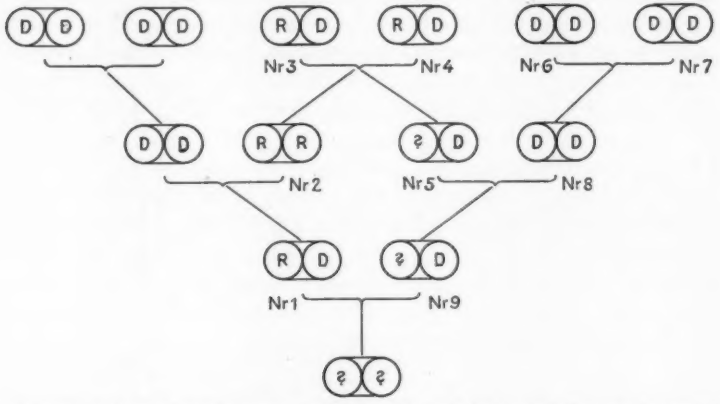

FIGURE 8.—Cousin marriage, one parent but no other relative having the recessive character.

1/3 free homozygotes (we exclude the possibility of their being character bearers). If No. 5 in 2/3 of the cases is a heterozygote, No. 9 in 2/6 of the cases is a heterozygote. The gene then has 2/12 possibilities of reaching a certain child in the marriage. The possibility of this child receiving the recessive gene from the other parent, who with certainty is a heterozygote, is 1/2. The probability for a coincidence of recessive genes in a marriage between cousins of this kind, consequently is $1/2\ 2/12 = 1/12$. Assuming, for instance, a case of some form of epilepsy, inheritable as a simple recessive character, an individual, who has a parent with the disease, would, on a fortuitously concluded marriage, run practically no risk of having children affected with the disease. Even if he entered into marriage with a cousin, the risk would of course be 0, if the diseased parent were that one

through whom he is not related to his cousin. If, on the other hand, that one of his parents through which he is related to his cousin, had epilepsy, the risk would be 1/12 that the children would suffer from epilepsy (assuming that the cousin to whom he is married, and the parents of the cousin, were healthy). The risk in a marriage between cousins under these conditions evidently is comparatively high.

Along these lines it should not be difficult to calculate the risk of a consanguineous marriage under certain given conditions. On the basis of such calculations it is possible to express a more definite opinion on the risk of a certain consanguineous marriage, than on the ground of general ideas regarding the harmfulness of consanguineous marriage in the presence of a recessive disposition for a disease in the family. Obviously, the more distant the disposition, the less is the increase of the risk in comparison with a normal marriage. If the disposition is to be found in near relatives, however, the increase of the risk for rare characters is very considerable.

Under these conditions it is, from the hereditary point of view, always to the advantage of the individual not to marry a relative, that is, if his children only are taken into account. With regard, however, to descendants in later generations the advantage of the individual marrying into the population is not so marked. To a certain extent the descendants in any case will be latent character bearers, and there is the risk that when they in their turn marry, they will marry another latent character bearer, the result being, perhaps, that suddenly they have a recessive character bearer among their offspring. The matter might perhaps be thus expressed that through a consanguineous marriage one takes the risk for one's own children, through marriage into the population that risk is transferred to later generations. Whichever is to be preferred, may to a certain extent be a matter of taste.

From the point of view of the community, the whole matter is of no great consequence. It should be remembered that consanguineous marriage hardly perceptibly alters the composition of the population. The increase of the number of recessive character bearers caused by consanguineous marriage, is very small relatively to the population. If the population is large, the increase may, however, comprise a not inconsiderable number of individuals.

Thus, consanguineous marriages are to some small extent unfavourable to the community. The case may, however, be reversed, if steps are taken to eradicate the disposition in question (by sterilizing the character bearers), or if the disease occasions lessened chances for marriage and reproduction, which would seem to be the case with most of the serious

hereditary diseases. In such case, consanguineous marriages might to some small extent be considered favourable, as the character then has a greater chance to meet in homozygous form, and as the character can only be eradicated in that form. To the community, therefore, it may be favourable that the character be brought together in homozygous form, the eradication proceeding quicker that way. (A similar argument can be advanced in regard to marriages between character bearers.)

Evidently, the conclusions reached in regard to the individual risk of consanguineous marriages, can inversely be applied in regard to favourable character bearers. The different probabilities calculated for different kinds of consanguineous marriages, obtain for recessive monoybrid characters, whether these are favourable or unfavourable.

From the point of view of the community, consanguineous marriages are, of course, to some small degree advantageous in the case of favourable characters. If the character bearers have lessened chances of reproduction, naturally inbreeding to a small extent occasions a speedier eradication of these characters in comparison to *panmixie*.

With regard to dominant characters, calculations on the effects of inbreeding are of little interest, as it can be seen directly on an individual if he possesses or does not possess such a factor. In the case of a rare character, it can in practice always be assumed that the character bearer is a heterozygote, if there are no special indications the other way. The risk of a consanguineous marriage, like that of other marriages, under these circumstances can be directly concluded from Mendel's law. For the population as a whole, inbreeding naturally entails a slightly reduced number of dominant character bearers, which, obviously, for the generation in question, is disadvantageous if the character is a favourable one, and *vice versa*.

The conclusion, whether inbreeding with its hardly perceptible effect, is to be considered advantageous or disadvantageous to a population, however, depends on the point of view from which the result is judged. Above, it has been shown that inbreeding, in the case of unfavourable characters, conditioning reduced possibilities of reproduction, results in a slightly speedier eradication of the character, than under *panmixie*. It has been pointed out that this *may* be advantageous, but it has not been said that under all circumstances this necessarily is so. Just as inbreeding is disadvantageous to the individual, it can also, from the point of the community, be said that inbreeding is disadvantageous, even though the unfavourable character bearers by it are a little more speedily eradicated. It all depends on the weighing of the present against

the future. Even if the gain is made that generations living in a far future, are free from unfavourable character bearers, it may be said that this advantage has been bought at a disproportionate price, at the cost of too many character bearers among the generations living nearer the present time. How much is to be sacrificed for future generations, always to a certain extent remains a question of opinion.

On the other hand, leaving time aside, and having the same regard for the individuals of future generations as for those living at this moment, there would seem to be a greater possibility of reaching an objective conclusion. Assuming that through very intense inbreeding, it would be possible in a comparatively short time to segregate the unfavourable characters to homozygosity, and practically eradicate them, the opposite eventuality is that character bearers arise through *panmixie*, and are eradicated more slowly. The effect of inbreeding as compared to *panmixie* then is dependent on the state of the population whether it is increasing, keeping constant, or decreasing. If the population speedily is increasing, undoubtedly it is advantageous to have a quicker eradication, which over a longer period will give a smaller number of character bearers, than a slower eradication. If, on the other hand, the size of the population is nearly constant, (really very slowly increasing) the number of character bearers in both cases will be exactly the same. At *panmixie* the character is never completely eradicated, not through inbreeding. The character bearers only will grow more and more rare, and the whole number, generation for generation, in each case will form an infinite series approaching the same limit. If, finally, the population is decreasing, the slower process is to be preferred, as giving a smaller total number of character bearers in all the generations, than the quicker process of eradication. (Formulas regarding this problem will be given in a paper appearing in Upsala Läkarförinings Förhandlingar.)

However, these arguments are chiefly of theoretical interest. The effect of inbreeding is so slight that in practice, and from the point of view of the population, it can be left out of account. As however, to a certain extent it is always a matter of opinion, whether a certain effect, however small, is to be regarded as of no consequence, I have thought it justifiable to put forth the above points of view, so much the more as consanguineous marriage to a certain degree is regulated by law. In many countries marriages between parents' sibs and sib's children are prohibited, in several cases without the possibility of exemption, and in some countries even more distant consanguinity is an obstacle to mar-

riage. As far as heredity is concerned, these inhibitions do not seem to be justified.

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STUDIES ON SELF-STERILITY. VIII. SELF-STERILITY ALLELOMORPHS.*

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INTRODUCTION

In a previous paper of this series (EAST AND MANGELSDORF 1926), the behavior of self-sterile plants of *Nicotiana Sanderæ* Hort. was interpreted by the reactions of 3 allelomorphs S_1, S_2, and S_3. The action of these allelomorphs was such that a plant of constitution $S_1 S_2$, when pollinated by pollen from a plant of constitution $S_2 S_3$, produced two types of progeny, $S_1 S_3$ and $S_2 S_3$, due to the slow growth of the pollen tubes bearing the factor S_2 (which was contained in the mother plant) as compared with the growth of the pollen tubes bearing the factor S_3. That these 3 factors were allelomorphic forms was shown by their ordinary behavior in crosses, and also (BRIEGER AND MANGELSDORF 1926) by the similar crossover values exhibited when a corolla-color factor *C* of the same linkage group was involved. Only the three allelomorphic factors were found in the material on hand,—material which had been inbred for several generations; but the results reported in an earlier paper (EAST AND PARK 1917) indicated that additional factors controlling self-sterility are present in *Nicotiana alata grandiflora*, in *Nicotiana Forgetiana*, and in the hybrids known as *Nicotiana Sanderæ*, which involve these two species.

Material was obtained from various seedsmen, therefore, for the purpose of isolating new factors, if such could be found. There were two objectives in view: first, to gather information as to the number of mutations that have taken place in the *S* locus; second, to find out whether mutations of a second locus are involved in controlling the behavior of self-sterility in these species. The second point has considerable theoretical importance. If mutations in a single locus will account for the genetic behavior of these self-sterile plants, obviously one may assume either that like factors inhibit pollen-tube growth or that unlike factors stimulate it. If two or more loci are involved, one must use the second postulate, since the plants used previously in studying the factors S_1, S_2, and S_3, must have been homozygous for self-sterility factors located in other loci.

* The GALTON AND MENDEL MEMORIAL FUND pays part of the cost of the accompanying tables.

EXPERIMENTAL WORK

The first lot of new material was grown from seed purchased at the firm of R. and J. Farquhar and Company of Boston. One packet of seed was marked *Sanderæ* hybrids, the other was marked *Nicotiana affinis* (=*Nicotiana alata grandiflora*). From among the plants obtained from the seed of the first packet, 4 individuals were investigated. One plant had a previously known genetic formula S_2S_3, as shown by sterility to pollen of S_2S_2, S_3S_3, and S_2S_3. The other 3 plants each contained the factor S_1; and, in addition, 2 of them contained a new factor S_4, while the third contained another new factor S_5. That is to say, by critical crossing tests, 1 plant was shown to be S_2S_3, 2 plants were shown to be S_1S_4, and 1 plant was shown to be S_1S_5. From the plants derived from the other packet, 2 were investigated. They proved to have the genetic formulas S_2S_6 and S_2S_7, respectively.

Thus there were 7 allelomorphs of the S factor which could be used in further tests. To make the proposed tests most effectively, plants were produced having the genetic formulæ S_1S_2, S_1S_3 . . . . S_1S_7. Seed was then obtained of *Sanderæ* hybrids and of *Affinis* hybrids from various sources, and 11 plants were selected for investigation. These 11 plants were crossed with the pollen from a plant having the genetic formula S_1S_1,—plants therefore which did not contain this particular factor. Each plant of the new material, since it was produced by natural pollination, could be assumed to be heterozygous for sterility factors. Any given population resulting from crossing a plant with S_1 pollen, therefore, should consist of equal numbers of plants S_1S_x and S_1S_y.

The sources of the 11 families thus produced were as follows:-

Family BA	Affinis hybrid	From Dreer
" BB	" "	" Mitchell
" BC	" "	" Dreer
" BD	Sanderæ "	" "
" BE	" "	" Vaughan
" BF	Affinis "	" "
" BG	Sanderæ "	" Dreer
" BH	" "	From Vaughan
" BI	" "	" "
" BK	" "	" Ferry
" BL	Affinis "	" Dreer

When these families began to blossom, a single vigorous plant from each was chosen as a tester (Type I). Each plant of the family was then pollinated with the pollen of that plant. As soon as a fertile union was obtained, the pollen of the second plant (Type II) was used on all of the

plants of the family. For example, all of the plants of Family BB were pollinated with pollen from BB2. The plants sterile with this pollen were assumed to have the genetic formula S_1S_z. But BB1 was fertile to the pollen from BB2. BB1, and all of the plants sterile to its pollen, were assumed, therefore, to have the genetic formula S_1S_y.

The results of the work in classifying the 11 families are shown in the tables 1 to 11. Fertility is designated +; sterility is designated −.

The behavior of Family BA, shown in table 1, is seen to be somewhat exceptional. The mother plant used in the production of the family was

TABLE 1.

Compatibilities of Family BA.

PLANT NUMBER	× BA2	× BA34	SELFED	PLANT NUMBER	× BA2	× BA34	SELFED
1	+	+	+	24	+	−	−
2	+	+	+	25	+	−	−
3	−	−	−	26	+	−	−
4	+	+	+	27	+	+	+
5	+	+	+	28	−	−	−
6	+	−	−	29	+	+	+
7	−	−	−	30	+	−	−
8	+	+	+	31	+	+	+
9	+	−	−	32	+	−	−
10	+	−	−	33	+	−	+
11	+	+	+	34	+	−	−
12	+	−	−	35	+	+	−
13	+	−	−	36	+	+	−
14	+	+	+	37	+	+	+
16	−	−	−	38	+	+	+
18	+	−	−	39	−	+	+
19	+	+	−	40	−	+	+
20	+	+	+	41	+	+	+
21	+	+	+	42	+	+	+
22	+	+	+	43	+	+	+
23	+	+	+				+

self-fertile, having the fertility which we have commonly called pseudo-fertility. The term is perhaps disengenuous, but nevertheless it has some merit. The difference between self-fertile plants and self-sterile plants depends upon rapidity of pollen-tube growth, and the speed at which pollen tubes bearing particular factors grow is dependent both upon subsidiary heritable factors and upon environmental conditions. For example, it will be shown in a later paper that *N. Langsdorffii* bears a factor belonging to the *S* series which we have called S_f. Now no subsidiary factors tending

to inhibit pollen-tube growth, even in combination with environmental conditions that are disadvantageous, are sufficient to prevent full complements of seed being formed after selfing. Factor S_f, therefore, may be termed a true factor for self-fertility. On the other hand, there are among the S factors several which produce such slow-growing pollen tubes that no combination of stimulating subsidiary heritable factors and optimum environmental conditions is sufficient to cause selfed seed to be produced. But between these two categories are S factors which are on the border line. When inhibiting subsidiary factors and poor environmental conditions (as

TABLE 2.

Compatibilities of Family BB.

PLANT NUMBER	× BB2	× BB1	SELFED	PLANT NUMBER	× BB2	BB1	SELFED
1	+	−	−	27	−	+	
2	−	+	−	28	+	−	−
3	+	−		29	+	−	
4	−	+	−	30	−	+	
5	−	+	−	31	+	−	−
6	+	−		32	+	−	−
7	−	+	−	33	+	−	−
8	−	+	−	34	−	+	
9	−	+		35	−	+	
10	+	−	−	36	−	+	
11	−	+	−	37	−	+	−
12	−	+		38	+	−	
13	−	+		39	+	−	
14	+	−	−	40	+	−	
15	−	+	−	41	+	−	
18	+	−		42	+	−	
19	+	−		43	+	−	
20	−	+		44	+	−	
21	−	+		45	+	−	
22	−	+	−	46	−	+	
23	−	+		47	+	−	
24	−	+		48	−	+	
25	+	−	−	49	−	+	
26	+	−	−	50	−	+	

low temperatures) are combined, no seed results; when accelerating subsidiary factors are combined with optimum environmental factors, seed is produced. This border line fertility we have called pseudo-fertility.

Plant A which served as the mother plant for Family BA was evidently of the latter type. Crossed with S_1S_1, it gave rise to a population consisting of two groups. There were 18 self-sterile plants and 23 self-fertile

plants. The self-fertile plants were fertile to the pollen of both BA2 and BA34, as would be expected,—with two exceptions. Plants 39 and 40 were sterile to BA2 pollen. Evidently there was just enough difference between plants 39 and 40 and the remaining plants of the group to inhibit the pollen-tube growth of pollen from BA2 sufficiently to prevent fertilization. The behavior of the 18 plants belonging to Type II was also slightly anomalous. It was to have been expected that all of these self-sterile plants would be

TABLE 3

Compatibilities of Family BC.

PLANT NUMBER	× BC1	× BC21	SELFED	PLANT NUMBER	× BC1	× BC21	SELFED
1	−	+		23	+	−	
2	+	−		24	−	+	
3	−	+		25	−	+	−
4	+	+	+[1]	26	−	+	−
5	−	+		27	−	+	−
6	−	+		28	−	+	−
7	+	−		29	−	+	
8	−	+	+[1]	30	−	+	
9	+	−		31	−	+	−
10	−	+	−	32	+	−	
11	−	+		33	−	+	−
12	+	−		34	+	−	
13	−	+		35	−	+	
14	+	−		36	−	+	−
15	+	−		37	−	+	
16	−	+	−	38	−	+	
17	−	+		39	+	−	
18	−	+		40	+	−	
19	−	+	−	41	+	−	
20	−	+		42	−	+	
21	+	−		43	−	+	
22	−	+					

[1] Pseudo-fertility small capsules.

fertile to the pollen of BA2 and sterile to the pollen of BA34. Actually, 13 plants behaved in this manner. In addition, plants 3, 7, 18, and 28 were sterile to both testers, while plant 19 was fertile to both testers. Plant 19 may belong to Type I, since it gave a small capsule on one self-pollination. The behavior of the other 4 plants is exceptional. Each was tested more that once with pollen of BA2 and the results were always negative. Possibly we have here a case in which plants of a given constitution are sterile to more than one *S* factor under the proper environmental condi-

tions and with the proper subsidiary factors; if so, it is something not found heretofore.

Family BB, (table 2), also an *Affinis* hybrid, had 48 plants which fell without exception into two groups. There were 23 plants fertile to BB2 and sterile to BB1. There were 25 plants sterile to BB2 and fertile to BB1. A random sample of 18 plants was selfed. Each proved to be self-sterile.

Family BC (table 3), an *Affinis* hybrid from Dreer, contained 43 plants. All of them appeared to be self-sterile, to judge from the small number of capsules that set naturally, with the exception of plants 4 and 8. These 2 plants produced the small capsules usually characteristic of pseudo-

TABLE 4

Compatibilities of Family BD.

PLANT NUMBER	× BD1	× BD44	SELFED	PLANT NUMBER	× BD1	× BD44	SELFED
1	−	+		26	+	−	
2	−	+		28	+	−	
3	−	+		29	−	+	
4	−	+		30	−	+	
5	+	−		31	+	−	
6	+	−		32	−	+	
7	−	+		33	+	−	
8	−	+		34	−	+	
9	+	−		35	−	+	
10	+	−		36	−	+	
12	−	+		37	−	+	
14	+	−		38	−	+	
15	−	+		39	+	−	
16	−	+		40	−	+	
17	−	+		41	−	+	
18	−	+		42	−	+	
19	+	−		43	+	−	
20	−	+		44	+	−	
21	−	+		45	−	+	
22	−	+		46	+	−	
23	+	−		47	−	−	
24	+	−		48	+	−	
25	+	−					

fertility. Plant 8 was sterile to the first tester BC1 and fertile to the second tester BC21. Plant 4, however, produced good capsules with both testers. The remaining 42 plants could be divided definitely into 2 groups. In the first group there are 29 plants, each sterile to BC1 and fertile to BC21. In the second group there are 13 plants, each fertile to BC1 and sterile to BC21.

Family BD (table 4) was produced by a *Sanderæ* hybrid from Dreer. It consisted of 45 plants. None were selfed, since—from the paucity of capsules set naturally—they all appeared to be self-sterile. One exceptional plant (No. 47) was repeatedly sterile to both testers, though the pollen appeared to be viable. We have no further information as to why it behaved in this manner. The cause may be connected with the self-sterility phenomena in some way not at present understood. But we are not limited

TABLE 5

Compatibilities of Family BE.

PLANT NUMBER	× BE1	× BE28	SELFED	PLANT NUMBER	× BE1	× BE28	SELFED
1	−	+		23	−	+	
2	−	+		24	−	+	
3	−	+	−	25	−	+	
4	+	−		26	+	−	
5	+	−		27	+	−	
6	−	+		28	+	−	
7	−	+		29	−	+	
8	−	+		30	−	+	
9	+	−		31	−	+	
10	+	−		32	+	−	−
11	−	+		33	−	+	
12	−	+		34	−	+	
13	−	+		35	+	−	
14	−	+		36	−	+	
15	−	+		38	+	−	
16	+	−		39	−	+	
17	+	−		40	−	+	
19	+	−		41	+	−	
20	−	+		42	+	−	
21	+	−		43	+	−	
22	−	+					

to such an interpretation. Occasional plants from material such as this show true male sterility. That is to say, they have defective pollen. And there is indication, though no critical proof, that somewhat more rarely female sterility is found. The remaining 44 plants fell into the usual 2 groups. There were 26 plants sterile to BD1 and fertile to BD44; there were 18 plants fertile to BD1 and sterile to BD44.

Family BE (Table 5) came from a *Sanderæ* hybrid from Vaughan. It consisted of 41 plants. The general appearance of the plants led us to believe that all were self-sterile, except possibly plants 3 and 32. These proved to be self-sterile. All of the plants fell into 2 groups: 24 were ste-

rile to BE1 and fertile to BE28; 17 were fertile to BE1 and sterile to BE28. It should be noted, however, that there was a little difficulty in classifying plants 21, 32, 34, and 38. Plants 21 and 38 produced seed in crosses with BE1, but the capsules were not as full of seed as would normally be expected. They were completely sterile with BE28. Plant 32 produced normal capsules with BE1. With BE28 a failure was recorded with one pollination and a small capsule with a second pollination. Plant 34 produced good capsules with BE28 and a small capsule with a few seeds with BE1.

TABLE 6

Compatibilities of Family BF.

PLANT NUMBER	× BF2	× BF13	SELFED	PLANT NUMBER	× BF2	× BF13	SELFED
1	+	−		23	−	+	
2	−	+		24	+	−	
3	+	−	−	25	+	−	
4	+	−		26	+	−	
5	−	+	−	27	+	−	
6	+	−	−	28	+	−	
7	+	−		29	+	−	
8	+	−	−	30	−	+	
10	+	−	−	31	+	−	
11	+	−		32	+	−	
12	+	−	−	33	+	−	
13	+	−	−	34	−	+	
14	+	−	−	36	+	−	
15	+	−		37	+	−	
16	−	+	−	38	+	−	
17	+	−	−	39	+	−	
18	−	+		40	−	−	
19	−	+	−	41	+	−	
20	−	+		42	−	+	
21	+	−		43	−	+	
22	+	−					

Family BF (table 6) coming from *Affinis* hybrids received from Vaughan, had one exceptional plant. Plant 40 was repeatedly sterile to both testers. The remaining 40 plants fell into two groups. There were 29 plants fertile with BF2 and sterile with BF13; there were 11 plants sterile with BF2 and fertile with BF13. Plants 17, 18, 29, and 37 required repeated tests to be certain of their classification. Plant 17 was fertile once and sterile once with pollen of BF2; it was always sterile with BF13. Plant 18 produced full capsules with BF13 and capsules with a few seeds with BF2. Plants

29 and 37 produced full capsules with BF2, and was sometimes sterile and sometimes partly fertile (few seeds) with BF13.

Family BG (table 7) consisting of 43 plants, was derived from seed of *Sanderæ* hybrids obtained from Dreer. Plant 13 was sterile twice with both testers. Plants 18 and 36, through some oversight were not tested with BG1. If one assumes that the sterility of these plants with pollen of BG32 is sufficient to classify them, then there are 16 plants sterile to BG1 and

TABLE 7

Compatibilities of Family BG.

PLANT NUMBER	× BG1	× BG32	SELFED	PLANT NUMBER	× BG1	× BG32	SELFED
1	−	+		23	+	−	
2	−	+		24	+	−	
3	−	+		25	+	−	=
4	+	−		26	−	+	
5	+	−		27	+	−	
6	−	+		28	+	−	
7	+	−		29	+	−	
8	+	−		30	+	−	
9	−	+		31	−	+	
10	−	+		32	+	−	
11	+	−		33	+	−	
12	+	−		34	−	+	
13	−	−		35	+	−	
14	−	+		36		−	
15	+	−		37	+	−	
16	−	+		38	−	+	
17	+	−		39	+	−	
18		−		40	+	−	
19	+	−		41	−	+	
20	−	+		42	−	+	
21	−	+		43	+	−	
22	+	−					

fertile to BG32, and 26 plants fertile to BG1 and sterile to BG32. Though the plants of this family all appeared to be self-sterile when judged by their ability to set capsules under natural conditions, undoubtedly there were some border line cases. For example, plant 25 gave full capsules with BG1 and proved to be self-sterile under test, but it also gave four partially filled capsules with BG32. Plant 38, which should have been fertile to BG32, having been sterile to BG1, gave one full capsule in one trial and failed to set in one trial. In addition, it should be noted that plants 3, 9, 14, and 34, which were always sterile to BG1, were not fully fertile to BG32. Each

was tested twice with BG32; and while all of the eight pollinations were positive, the capsules were never full of seed.

Family BH (table 8) was derived from the *Sanderæ* hybrids of Vaughan. It consisted of 42 plants, of which 24 were sterile to BH3 and fertile to BH21, and 18 were fertile to BH3 and sterile to BH21. All appeared to be

TABLE 8

Compatibilities of Family BH.

PLANT NUMBER	× BH3	× BH21	SELFED	PLANT NUMBER	× BH3	× BH21	SELFED
1	−	+		22	+	−	
2	−	+		23	−	+	
3	−	+		24	+	−	
4	−	+		25	−	+	
5	+	−		26	−	+	
6	+	−		27	+	−	
7	+	−		28	+	−	
8	+	−		29	+	−	
9	−	+		30	−	+	
10	−	+		31	−	+	
11	−	+		32	−	+	
12	+	−		33	+	−	
13	−	+		34	−	+	
14	+	−		35	−	+	
15	−	+		36	+	−	
16	−	+		37	+	−	
17	−	+		38	+	−	
18	−	+		39	−	+	
19	+	−		40	−	+	
20	−	+		41	−	+	
21	+	−		32	+	−	

self-sterile. In fact, plant 33 was the only plant that showed a slight evidence of pseudo-fertility. The only difficulties encountered in trying to classify the plants of this family were with plants 19, 24, 30, and 33, which had to be tested twice in order to establish their compatibilities in an unmistakable manner.

Family BI (table 9) from Vaughan's stock of *Sanderæ* hybrids, consisted of 50 plants, all of which appeared to be self-sterile. A sample of 9 plants proved to be self-sterile. The plants could be divided into 2 groups without difficulty. There were 30 plants sterile to BI1 and fertile to BI32, and 20 plants fertile to BI1 and sterile to BI32.

Family BK (table 10), from *Sanderæ* hybrid seed of Ferry, consisted of 42 plants. BK1 which was used as one of the testers, exhibited some

pseudo-fertility. It gave a small capsule when selfed. Plants 30, 32, and 33 also showed some pseudo-fertility,—the first and the third yielding small capsules when selfed. These three were the only plants besides BK1 which showed noticeable self-fertility. All three were fertile with both BK3 and BK1; but, judging both from the size of capsules produced after pollination with BK1 as compared with those produced after pollination with BK3, and from the behavior of the four plants (including BK1) when selfed they should be classified as belonging to the type represented by BK1.

TABLE 9

Compatibilities of Family BI.

PLANT NUMBER	× BI1	× BI32	SELFED	PLANT NUMBER	× BI1	× BI32	SELFED
1	−	+	−	26	−	+	
2	+	−	−	27	+	−	
3	−	+	−	28	−	+	
4	−	+	−	29	+	−	
5	−	+		30	+	−	
6	−	+	−	31	−	+	
7	−	+	−	32	+	−	
8	+	−	−	33	+	−	
9	−	+	−	34	−	+	
10	+	−	−	35	+	−	
11	+	−		36	+	−	
12	−	+		37	+	−	
13	+	−		38	−	+	
14	−	+		39	+	−	
15	−	+		40	−	+	
16	−	+		41	−	+	
17	−	+		42	−	+	
18	−	+		43	−	+	
19	+	−		44	−	+	
20	+	−		45	−	+	
21	−	+		47	+	−	
22	−	+		48	−	+	
23	−	+		49	+	−	
24	−	+		50	+	−	
25	+	−		51	−	+	

Omitting these three plants, however, there are two groups, one of 20 plants fertile to BK3 and sterile to BK1, and one of 18 plants sterile to BK3 and fertile to BK1. In addition, it may be noted that plants 39 and 40 showed a slight pseudo-fertility in one pollination with BK1 and complete sterility in a second pollination. Likewise, plants 6, 13, 14 and 20 exhibited a slight degree of pseudo-fertility with BK3.

TABLE 10
Compatibilities of Family BK.

PLANT NUMBER	× BK3	× BK1	SELFED	PLANT NUMBER	× BK3	× BK1	SELFED
1	+	+	−	23	+	−	
2	+	−		24	+	−	
3	−	+		25	−	+	
4	+	−		26	+	−	
5	+	−		27	+	−	
6	−	+		28	−	+	
7	+	−		29	−	+	
8	+	−		30	+	+	+
9	+	−		31	−	+	
10	−	+		32	+	+	−
12	+	−		33	+	+	+
13	−	+		34	+	−	
14	−	+		35	+	−	
15	−	+		36	−	+	
16	−	+		37	−	+	
17	−	+		38	+	−	
18	−	+		39	+	−	
19	+	−		40	+	−	
20	−	+		41	−	+	
21	+	−		42	+	−	
22	−	+		43	+	−	

TABLE 11
Compatibilities of Family BL.

PLANT NUMBER	× BL1	× BL31	SELFED	PLANT NUMBER	× BL1	× BL31	SELFED
1	−	+		23	−	+	
2	−	+		24	−	+	
3	+	−		25	−	+	−
4	+	−		26	+	−	
5	+	−		27	+	−	
7	−	+		28	−	+	
8	−	+		29	−	+	
9	−	+		30	+	−	−
10	+	−		31	+	−	
11	−	+		32	+	−	−
12	−	+		33	−	+	
14	+	−		34	−	+	
15	−	+		35	+	−	
16	−	+		36	−	+	
18	+	−		37	+	−	
19	+	−	−	38	−	+	
20	+	−		39	+	−	
21	+	−		40	+	−	
22	+	−		41	+	−	

Family BL (table 11), was derived from the *Affinis* hybrids of Dreer. From their behavior all of the 38 plants constituting the population were self-sterile although only 4 were tested. No anomalous behavior and no pseudo-fertility was recorded. There were 18 plants sterile to BL1 and fertile to BL31 and 20 plants fertile to BL1 and sterile to BL31.

The data on the B families show that the 11 individuals chosen for crossing with S_1S_1 were heterozygous for definite S factors,—that is that their genetic formulæ as regards self-sterility were S_xS_y, S_wS_z, and so forth. Each family consisted of two groups containing approximately equal numbers of individuals. This is seen to be the case when one compares the family groups with the probable errors expressed in numbers of individuals, as follows:-

Family	*Numbers of each type*	*Deviation from equality*	*P. E. in Numbers*
BA	18–23	2.5	2.2
BB	23–25	1.0	2.3
BC	29–13	8.0	2.2
BD	26–28	4.0	2.2
BE	24–17	3.5	2.2
BF	29–11	9.0	2.1
BG	16–26	5.0	2.2
BH	24–18	3.0	2.2
BI	20–30	5.0	2.4
BK	20–18	1.0	2.1
BL	18–20	1.0	2.1

Of the 11 families, the deviations of the two groups from equality is less than .5 P. E. in 3 families, slightly over 1.0 P. E. in 1 family, less than 2.0 P. E. in 3 families, slightly over 2.0 P. E. in 2 families, over 3.0 P. E. in 1 family, and over 4.0 P. E. in the family showing the greatest discrepancy.

The next point in the investigation was to try to distinguish the different S factors in the various groups. BA Type I, afterwards called BA-I, was tested with BA-II, with the two types of the other 10 families, and with the seven other testers, S_1S_2 . . . . S_1S_7. It showed fertility in every test. Since the plants of BA-I were self-fertile it may seem queer to call its S factor S_{15}; but there seems to be no good reason for not so doing. The behavior of S_{15} is merely an extreme case of rapid pollen-tube growth which is uninhibited in styles of plants bearing the same factor. From the different source of the material, we believe that the S_f factor borne by *N. Langsdorffii* is probably different from S_{15}; but there is no way of proving the matter.

Table 12 shows the tests made with the plants of Family BA, Type II. It will be noted that there were two cases of incompatibility. Plant BA-II-

12 was sterile to the pollen of plant BE-II-28; and plant BA-II-6 was sterile to the pollen of BG-II-32. Two additional pollinations for each of these combinations confirmed the result. We may take it, then, that

TABLE 12

Tests of Family BA.

TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT
BA-II-34	BA-II-32	−
BA-II-12	BB-I-2	+
BA-II-12	BB-II-1	+
BA-II-12	BC-I-1	+
BA-II-12	BC-II-21	+
BA-II-12	BD-I-1	+
BA-II-12	BD-II-44	+
BA-II-12	BE-I-1	+
BA-II-12	BE-II-28	−
BA-II-12	BF-I-2	+
BA-II-12	BF-II-13	+
BA-II-12	BG-I-1	+
BA-II-6	BG-II-32	−
BA-II-6	BH-I-3	+
BA-II-6	BH-II-21	+
BA-II-6	BI-I-1	+
BA-II-9	BI-II-32	+
BA-II-9	BK-I-3	+
BA-II-9	BK-II-1	+
BA-II-9	BL-I-1	+
BA-II-9	BL-II-31	+
BA-II-34	S1S2	+
BA-II-41	S1S2	+
BA-II-34	S1S3	+
BA-II-41	S1S3	+
BA-II-34	S1S4	+
BA-II-41	S1S4	+
BA-II-34	S1S5	+
BA-II-41	S1S5	+
BA-II-34	S1S6	+
BA-II-41	S1S6	+
BA-II-34	S1S7	+
BA-II-41	S1S7	+

BA-II, BE-II, and BG-II have a common sterility factor which can be designated S_8. In other words, the plants of these groups are S_1S_8. Naturally, we look for confirmation of the conclusion by examining other unions where any 2 plants of these 3 groups are involved. In table 16 are found

combinations BE-II-28 BA-II-32 and BE-II-42 BG-II-32 while in table 18 are found combinations BG-II-43 BA-II-32 and BG-II-43 BE-II-28 all show incompatibility as expected.

In table 13 are the tests on Family BB. Among the combinations made with Type I are 2 tests with plants having the genetic formula S_1S_5. One was fertile, one was sterile. Other tests, however, show that the single failure with S_1S_5 was accidental. For example, combinations made with

TABLE 13

Tests of Family BB.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BB-I-2	BA-I-2	+	BB-II-1	BA-I-2	+
BB-I-4	BA-II-32	+	BB-II-1	BA-II-32	+
BB-I-2	BB-I-2	−	BB-II-1	BB-I-2	+
BB-I-2	BB-II-1	+	BB-II-1	BB-II-1	−
BB-I-2	BC-I-1	+	BB-II-1	BC-I-1	+
BB-I-2	BC-II-21	+	BB-II-1	BC-II-21	+
BB-I-2	BD-I-1	+	BB-II-1	BD-I-1	+
BB-I-2	BD-II-44	+	BB-II-1	BD-II-44	+
BB-I-2	BE-I-1	+	BB-II-1	BE-I-1	+
BB-I-2	BE-II-28	+	BB-II-3	BE-II-28	+
BB-I-2	BF-I-2	+	BB-II-3	BF-I-2	+
BB-I-2	BF-II-13	+	BB-II-3	BF-II-13	+
BB-I-2	BG-I-1	+	BB-II-3	BG-I-1	+
BB-I-4	BG-II-32	+	BB-II-6	BG-II-32	+
BB-I-4	BH-I-3	+	BB-II-6	BH-I-3	+
BB-I-4	BH-II-21	+	BB-II-6	BH-II-21	+
BB-I-4	BI-I-1	+	BB-II-6	BI-I-1	+
BB-I-4	BI-II-32	+	BB-II-6	BI-II-32	−
BB-I-4	BK-I-3	+	BB-II-6	BK-I-3	+
BB-I-4	BK-II-1	+	BB-II-6	BK-II-1	+
BB-I-4	BL-I-1	+	BB-II-6	BL-I-1	+
BB-I-4	BL-II-31	−	BB-II-6	BL-II-31	+
BB-I-4	S1S2	+	BB-II-1	S1S2	+
BB-I-7	S1S2	+	BB-II-10	S1S2	+
BB-I-4	S1S3	+	BB-II-1	S1S3	+
BB-I-7	S1S3	+	BB-II-10	S1S3	+
BB-I-4	S1S4	+	BB-II-1	S1S4	+
BB-I-7	S1S4	+	BB-II-10	S1S4	+
BB-I-4	S1S5	+	BB-II-1	S1S5	−
BB-I-7	S1S5	−	BB-II-10	S1S5	+
BB-I-4	S1S6	−	BB-II-1	S1S6	+
BB-I-7	S1S6	−	BB-II-10	S1S6	+
BB-I-4	S1S7	+	BB-II-1	S1S7	+
BB-I-7	S1S7		BB-II-10	S1S7	+

plants from BB-II and from BI-II, which are later shown to be S_1S_5, are fertile. The only true incompatibility of BB-I is with S_1S_6 and with BL-II-31. And BL-II is also shown to be S_1S_6 by the tests of table 22. BB-II plants have the formula S_1S_5. Plant BB-II-6 is sterile to pollen of BI-II-32. The reciprocal is also sterile as is seen in table 20. It is true that one test with S_1S_5 showed fertility and one test showed sterility. But additional tests not shown in the table confirmed the fact that BB-II is in truth S_1S_5 and is incompatible with S_1S_5 plants. There were 3 more

TABLE 14

Tests of Family BC.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BC-I-3	BA-II-32	+	BC-II-21	BA-II-32	+
BC-I-1	BB-I-2	+	BC-II-2	BB-I-2	+
BC-I-1	BB-II-1	+	BC-II-2	BB-II-1	+
BC-I-1	BC-I-1	−	BC-II-2	BC-I-1	+
BC-I-1	BC-II-21	+	BC-II-2	BC-II-21	−
BC-I-1	BD-I-1	+	BC-II-2	BD-I-1	−
BC-I-1	BD-II-44	+	BC-II-2	BD-II-44	+
BC-I-1	BE-I-1	+	BC-II-2	BE-I-1	+
BC-I-22	BE-II-28	+	BC-II-23	BE-II-28	+
BC-I-22	BF-I-2	+	BC-II-23	BF-I-2	+
BC-I-22	BF-II-13	+	BC-II-23	BF-II-13	+
BC-I-22	BG-I-1	+	BC-II-23	BG-I-1	+
BC-I-22	BG-II-32	+	BC-II-23	BG-II-32	+
BC-I-22	BH-I-3	+	BC-II-23	BH-I-3	+
BC-I-22	BH-II-21	+	BC-II-23	BH-II-21	+
BC-I-22	BI-I-1	+	BC-II-23	BI-I-1	+
BC-I-22	BI-II-32	+	BC-II-23	BI-II-32	+
BC-I-22	BK-I-3	+	BC-II-23	BK-I-3	+
BC-I-22	BK-II-1	+	BC-II-23	BK-II-1	+
BC-I-22	BL-I-1	+	BC-II-23	BL-I-1	+
BC-I-22	BL-II-31	+	BC-II-23	BL-II-31	+
BC-I-3	S1S2	−	BC-II-21	S1S2	+
BC-I-42	S1S2	−	BC-II-41	S1S2	+
BC-I-3	S1S3	+	BC-II-21	S1S3	+
BC-I-42	S1S3	+	BC-II-41	S1S3	+
BC-I-3	S1S4	+	BC-II-21	S1S4	+
BC-I-42	S1S4	+	BC-II-41	S1S4	+
BC-I-3	S1S5	+	BC-II-21	S1S5	+
BC-I-42	S1S5	+	BC-II-41	S1S5	+
BC-I-3	S1S6	+	BC-II-21	S1S6	+
BC-I-42	S1S6	+	BC-II-41	S1S6	+
BC-I-3	S1S7	+	BC-II-1	S1S7	+
BC-I-42	S1S7	+	BC-II-41	S1S7	+

tests with the pollen of S_1S_5 and 2 reciprocal tests in which S_1S_5 was used as the mother. All failed.

The tests of Family BC are shown in table 14. Incompatibility of Type BC-I was shown only with S_1S_2. Two additional tests not shown in the table were made with the pollen of S_1S_2. Two reciprocal tests were also made. In each test failure was recorded. The plants of BC-I, therefore, have the genetic constitution S_1S_2. The only incompatibility exhibited by plants of BC-II is with BD-I-1. The reciprocal combination also failed

TABLE 15

Tests of Family BD.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BD-I-1	BA-II-32	+	BD-II-26	BA-II-32	+
BD-I-1	BB-I-2	+	BD-II-26	BB-I-2	+
BD-I-1	BB-II-1	+	BD-II-26	BB-II-1	+
BD-I-1	BC-I-1	+	BD-II-26	BC-I-1	+
BD-I-1	BC-II-21	−	BD-II-26	BC-II-21	+
BD-I-1	BD-I-1	−	BD-II-26	BD-I-1	+
BD-I-1	BD-II-44	+	BD-II-26	BD-II-44	−
BD-I-1	BE-I-1	+	BD-II-26	BE-I-1	+
BD-I-1	BE-II-28	+	BD-II-26	BE-II-28	+
BD-I-1	BF-I-2	+	BD-II-26	BF-I-2	+
BD-I-1	BF-II-13	+	BD-II-26	BF-II-13	+
BD-I-1	BG-I-1	+	BD-II-26	BG-I-1	+
BD-I-1	BG-II-32	+	BD-II-26	BG-II-32	+
BD-I-1	BH-I-3	+	BD-II-26	BH-I-3	+
BD-I-1	BH-II-21	+	BD-II-26	BH-II-21	+
BD-I-1	BI-I-1	+	BD-II-26	BI-I-1	+
BD-I-1	BI-II-32	+	BD-II-26	BI-II-32	+
BD-I-1	BK-I-3	+	BD-II-26	BK-I-3	+
BD-I-1	BK-II-1	+	BD-II-26	BK-II-1	−
BD-I-1	BL-I-1	+	BD-II-26	BL-I-1	+
BD-I-1	BL-II-31	+	BD-II-26	BL-II-31	−
BD-I-1	S1S2	+	BD-II-26	S1S2	+
BD-I-45	S1S2	+	BD-II-44	S1S2	+
BD-I-1	S1S3	+	BD-II-26	S1S3	+
BD-I-45	S1S3	+	BD-II-44	S1S3	+
BD-I-1	S1S4	+	BD-II-26	S1S4	+
BD-I-45	S1S4	+	BD-II-44	S1S4	+
BD-I-1	S1S5	+	BD-II-26	S1S5	+
BD-I-45	S1S5	+	BD-II-44	S1S5	+
BD-I-1	S1S6		BD-II-26	S1S6	+
BD-I-45	S1S6		BD-II-44	S1S6	+
BD-I-1	S1S7		BD-II-26	S1S7	+
BD-I-45	S1S7		BD-II-44	S1S7	+

(table 15). The plants of this group, then, can be given the formula S_1S_9.

In table 15 are the tests of Family BD. As is to be expected from the results of table 14, BD-I plants show incompatibility only with BC-II. Since the test plants BD-I-1 and BD-I-45 died before they could be tested with S_1S_6 and S_1S_7, it is a fair question to ask how we know that they do not belong to either of these groups. The reason is that BD-I plants were tested reciprocally with plants of BB-I and BL-II, two groups having the constitution S_1S_6; and were further tested with plants of BG-I and BK-I,

TABLE 16

Tests of Family BE.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BE-I-30	BA-II-32	+	BE-II-28	BA-II-32	−
BE-I-1	BB-I-2	+	BE-II-43	BB-I-2	+
BE-I-1	BB-II-1	+	BE-II-43	BB-II-1	+
BE-I-1	BC-I-1	+	BE-II-43	BC-I-1	+
BE-I-1	BC-II-21	+	BE-II-43	BC-II-21	+
BE-I-1	BD-I-1	+	BE-II-43	BD-I-1	+
BE-I-1	BD-II-44	+	BE-II-43	BD-II-44	+
BE-I-1	BE-I-1	−	BE-II-43	BE-I-1	+
BE-I-1	BE-II-28	+	BE-II-43	BE-II-28	−
BE-I-1	BF-I-2	−	BE-II-43	BF-I-2	+
BE-I-1	BF-II-13	+	BE-II-43	BF-II-13	+
BE-I-1	BG-I-1	+	BE-II-43	BG-I-1	+
BE-I-1	BG-II-32	+	BE-II-42	BG-II-32	−
BE-I-1	BH-I-3	+	BE-II-42	BH-I-3	+
BE-I-1	BH-II-21	+	BE-II-42	BH-II-21	+
BE-I-1	BI-I-1	+	BE-II-42	BI-I-1	+
BE-I-2	BI-II-32	+	BE-II-43	BI-II-32	+
BE-I-2	BK-I-3	+	BE-II-43	BK-I-3	+
BE-I-2	BK-II-1	+	BE-II-43	BK-II-1	+
BE-I-2	BL-I-1	+	BE-II-43	BL-I-1	+
BE-I-1	BL-II-31	+	BE-II-43	BL-II-31	+
BE-I-30	S1S2	+	BE-II-27	S1S2	+
BE-I-31	S1S2	+	BE-II-28	S1S2	+
BE-I-30	S1S3		BE-II-27	S1S3	+
BE-I-31	S1S3	+	BE-II-28	S1S3	+
BE-I-30	S1S4	+	BE-II-27	S1S4	+
BE-I-31	S1S4	+	BE-II-28	S1S4	+
BE-I-30	S1S5	+	BE-II-27	S1S5	+
BE-I-31	S1S5	+	BE-II-28	S1S5	+
BE-I-30	S1S6	+	BE-II-27	S1S6	+
BE-I-31	S1S6	+	BE-II-28	S1S6	+
BE-I-30	S1S7	+	BE-II-27	S1S7	+
BE-I-31	S1S7	+	BE-II-28	S1S7	+

two groups having the constitution S_1S_7. All of these combinations were fertile. BD-II plants are shown to have the constitution S_1S_{10}. They are persistently sterile only with plants from the group BK-II, other pollinations not shown in the table having been made as a check. It is true that BD-II-26 was sterile to the pollen of BL-II-31 (2 pollinations); but there is reason to believe that this single outstanding exception in the extensive crosses among the plants of the B families was due to particulate tru sterility of flowers of a certain branch of plant BL-II-31. In the first place,

TABLE 17

Tests of Family BF.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BF-I-23	BA-II-32	+	BF-II-22	BA-II-32	+
BF-I-2	BB-I-2	+	BF-II-13	BB-I-2	+
BF-I-2	BB-II-1	+	BF-II-13	BB-II-1	+
BF-I-2	BC-I-1	+	BF-II-13	BC-I-1	+
BF-I-2	BC-II-21	+	BF-II-13	BC-II-21	+
BF-I-2	BD-I-1	+	BF-II-13	BD-I-1	+
BF-I-2	BD-II-44	+	BF-II-13	BD-II-44	+
BF-I-2	BE-I-1	−	BF-II-13	BE-I-1	+
BF-I-2	BE-II-28	+	BF-II-13	BE-II-28	+
BF-I-2	BF-I-2	−	BF-II-13	BF-I-2	+
BF-I-2	BF-II-13	+	BF-II-13	BF-II-13	−
BF-I-2	BG-I-1	+	BF-II-13	BG-I-1	+
BF-I-2	BG-II-32	+	BF-II-15	BG-II-32	+
BF-I-2	BH-I-3	+	BF-II-15	BH-I-3	+
BF-I-2	BH-II-21	+	BF-II-15	BH-II-21	+
BF-I-2	BI-I-1	+	BF-II-15	BI-I-1	+
BF-I-2	BI-II-32	+	BF-II-15	BI-II-32	+
BF-I-2	BK-I-3	+	BF-II-15	BK-I-3	+
BF-I-2	BK-II-1	+	BF-II-15	BK-II-1	+
BF-I-2	BL-I-1	+	BF-II-15	BL-I-1	+
BF-I-2	BL-II-31	+	BF-II-15	BL-II-31	+
BF-I-23	S1S2	+	BF-II-22	S1S2	+
BF-I-43	S1S2	+	BF-II-41	S1S2	+
BF-I-23	S1S3	+	BF-II-22	S1S3	+
BF-I-43	S1S3	+	BF-II-41	S1S3	+
BF-I-23	S1S4	+	BF-II-22	S1S4	+
BF-I-43	S1S4	+	BF-II-41	S1S4	+
BF-I-23	S1S5	+	BF-II-22	S1S5	+
BF-I-43	S1S5	+	BF-II-41	S1S5	+
BF-I-23	S1S6	+	BF-II-22	S1S6	+
BF-I-43	S1S6	+	BF-II-41	S1S6	+
BF-I-23	S1S7	+	BF-II-22	S1S7	+
BF-I-43	S1S7	+	BF-II-41	S1S7	+

the reciprocal of this type of mating, BL-II-4×BD-II-44, was fertile. Moreover, several critical tests show that BL-II plants have the formula S_1S_6, as do the plants of BB-I; yet no other plants of the group S_1S_6, are sterile to plants of BD-II.

Table 16 shows the tests of Family BE. BE-I plants can be given the formula S_1S_{11}. They are sterile only to the pollen of BF-I. The reciprocal is also sterile (table 17). Plant BE-I-30 died before it could be tested against S_1S_3; but BE-I-31 was fertile with S_1S_3 and BE-I-1 was fertile

TABLE 18

Tests of Family BG.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BG-I-31	BA-II-32	+	BG-II-43	BA-II-32	−
BG-I-1	BB-I-2	+	BG-II-43	BB-I-2	+
BG-I-1	BB-II-1	+	BG-II-43	BB-II-1	+
BG-I-1	BC-I-1	+	BG-II-43	BC-I-1	+
BG-I-1	BC-II-21	+	BG-II-43	BC-II-21	+
BG-I-1	BD-I-1	+	BG-II-43	BD-I-1	+
BG-I-1	BD-II-44	+	BG-II-43	BD-II-44	+
BG-I-1	BE-I-1	+	BG-II-43	BE-I-1	+
BG-I-2	BE-II-28	+	BG-II-43	BE-II-28	−
BG-I-2	BF-I-2	+	BG-II-43	BF-I-2	+
BG-I-1	BF-II-13	+	BG-II-43	BF-II-13	+
BG-I-1	BG-I-1	−	BG-II-43	BG-I-1	+
BG-I-42	BG-II-32	+	BG-II-4	BG-II-32	−
BG-I-42	BH-I-3	+	BG-II-4	BH-I-3	+
BG-I-42	BH-II-21	+	BG-II-4	BH-II-21	+
BG-I-42	BI-I-1	+	BG-II-4	BI-I-1	+
BG-I-42	BI-II-32	+	BG-II-43	BI-II-32	+
BG-I-42	BK-I-3	−	BG-II-43	BK-I-3	+
BG-I-42	BK-II-1	+	BG-II-43	BK-II-1	+
BG-I-42	BL-I-1	+	BG-II-43	BL-I-1	+
BG-I-41	BL-II-31	+	BG-II-40	BL-II-31	+
BG-I-31	S1S2	+	BG-II-32	S1S2	+
BG-I-42	S1S2	+	BG-II-43	S1S2	+
BG-I-31	S1S3	+	BG-II-32	S1S3	+
BG-I-42	S1S3	+	BG-II-43	S1S3	+
BG-I-31	S1S4	+	BG-II-32	S1S4	+
BG-I-42	S1S4	+	BG-II-43	S1S4	+
BG-I-31	S1S5	+	BG-II-32	S1S5	+
BG-I-42	S1S5	+	BG-II-43	S1S5	+
BG-I-31	S1S6	+	BG-II-32	S1S6	+
BG-I-42	S1S6	+	BG-II-43	S1S6	+
BG-I-31	S1S7	−	BG-II-32	S1S7	+
BG-I-42	S1S7	−	BG-II-43	S1S7	+

with BL-I-1, (also S_1S_4). BE-II plants proved to be S_1S_8. They were sterile reciprocally with BA-II plants and with BG-II plants,—these last two groups being incompatible with each other, as expected.

In table 17 the results of the tests with Family BF are recorded. BF-I plants, as already noted, have the constitution S_1S_{11}. They belong to the same group as the plants of BE-I. All other combinations are fertile. The plants of BF-II are fertile to the plants of all other groups. They are designated S_1S_{12}.

TABLE 19

Tests of Family BH.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BH-I-2	BA-II-32	+	BH-II-29	BA-II-32	+
BH-I-1	BB-I-2	+	BH-II-42	BB-I-2	+
BH-I-1	BB-II-1	+	BH-II-42	BB-II-1	+
BH-I-1	BC-I-1	+	BH-II-42	BC-I-1	+
BH-I-1	BC-II-21	+	BH-II-42	BC-II-21	+
BH-I-1	BD-I-1	+	BH-II-42	BD-I-1	+
BH-I-1	BD-II-44	+	BH-II-42	BD-II-44	+
BH-I-1	BE-I-1	+	BH-II-42	BE-I-1	+
BH-I-3	BE-II-28	+	BH-II-42	BE-II-28	+
BH-I-3	BF-I-2	+	BH-II-42	BF-I-2	+
BH-I-3	BF-II-13	+	BH-II-42	BF-II-13	+
BH-I-3	BG-I-1	+	BH-II-42	BG-I-1	+
BH-I-41	BG-II-32	+	BH-II-42	BG-I-32	+
BH-I-41	BH-I-3	−	BH-II-42	BH-I-3	+
BH-I-41	BH-II-21	+	BH-II-42	BH-II-21	−
BH-I-41	BI-I-1	+	BH-II-42	BI-I81	+
BH-I-40	BI-II-32	+	BH-II-38	BI-II-32	+
BH-I-40	BK-I-3	+	BH-II-38	BK-I-3	+
BH-I-40	BK-II-1	+	BH-II-38	BK-II-I1	+
BH-I-40	BL-I-1	+	BH-II-38	BL-I-1	+
BH-I-41	BL-II-31	+	BH-II-38	BL-II-31	+
BH-I-1	S1S2	+	BH-II-28	S1S2	+
BH-I-2	S1S2	+	BH-II-29	S1S2	+
BH-I-1	S1S3	+	BH-II-28	S1S3	+
BH-I-2	S1S3	+	BH-II-29	S1S3	+
BH-I-1	S1S4	+	BH-II-28	S1S4	−
BH-I-2	S1S4	+	BH-II-29	S1S4	−
BH-I-1	S1S5	+	BH-II-28	S1S5	+
BH-I-2	S1S5	+	BH-II-29	S1S5	+
BH-I-1	S1S6	+	BH-II-28	S1S6	+
BH-I-2	S1S6	+	BH-II-29	S1S6	+
BH-I-1	S1S7	+	BH-II-28	S1S7	+
BH-I-2	S1S7	+	BH-II-29	S1S7	+

Table 18 shows the results of the tests with Family BG. BG-I plants are S_1S_7, as shown by their incompatibility with the pollen of S_1S_7. S_1S_7 plants were also found to be sterile to the pollen of BG-I plants in 4 tests. BG-I-42 was also sterile to BK-I-3, another S_1S_7 group. This last combination was made with negative results in 3 other cases not recorded in the table. All other combinations were fertile. BG-II plants were fertile in all combinations except those with BA-II and BE-II. This group, therefore, is S_1S_8.

Table 19 shows the results of the tests with Family BH. The plants of

TABLE 20

Tests of Family BI.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BI-I-1	BA-II-32	+	BI-II-13	BA-II-32	+
BI-I-1	BB-I-2	+	BI-II-2	BB-I-2	+
BI-I-1	BB-II-1	+	BI-II-2	BB-II-1	−
BI-I-1	BC-I-1	+	BI-II-2	BC-I-1	+
BI-I-1	BC-II-21	+	BI-II-2	BC-II-21	+
BI-I-1	BD-I-1	+	BI-II-2	BD-I-1	+
BI-I-1	BD-II-44	+	BI-II-2	BD-II-44	+
BI-I-1	BE-I-1	+	BI-II-2	BE-I-1	+
BI-I-51	BE-II-28	+	BI-II-50	BE-II-28	+
BI-I-51	BF-I-2	+	BI-II-50	BF-I-2	+
BI-I-51	BF-II-13	+	BI-II-50	BF-II-13	+
BI-I-51	BG-I-1	+	BI-II-50	BG-I-1	+
BI-I-51	BG-II-32	+	BI-II-50	BG-II-32	+
BI-I-51	BH-I-3	+	BI-II-50	BH-I-3	+
BI-I-51	BH-II-21	+	BI-II-50	BH-II-21	+
BI-I-51	BI-I-1	−	BI-II-50	BI-I-1	+
BI-I-51	BI-II-32	+	BI-II-50	BI-II-32	−
BI-I-51	BK-I-3	+	BI-II-50	BK-I-3	+
BI-I-51	BK-II-1	+	BI-II-50	BK-II-1	+
BI-I-51	BL-I-1	+	BI-II-50	BL-I-1	+
BI-I-51	BL-II-31	+	BI-II-50	BL-II-31	+
BI-I-1	S1S2	+	BI-II-13	S1S2	+
BI-I-12	S1S2	+	BI-II-25	S1S2	+
BI-I-1	S1S3	+	BI-II-13	S1S3	+
BI-I-12	S1S3	+	BI-II-25	S1S3	+
BI-I-1	S1S4	+	BI-II-13	S1S4	+
BI-I-12	S1S4	+	BI-II-25	S1S4	+
BI-I-1	S1S5	+	BI-II-13	S1S5	−
BI-I-12	S1S5	+	BI-II-25	S1S5	−
BI-I-1	S1S6	+	BI-II-13	S1S6	+
BI-I-12	S1S6	+	BI-II-25	S1S6	+
BI-I-1	S1S7	+	BI-II-13	S1S7	+
BI-I-12	S1S7		BI-II-25	S1S7	+

BH-I are S_1S_{13}. They are fertile in all combinations with the other groups. The plants of BH-II are S_1S_4. They show sterility with the pollen of S_1S_4 as recorded. An S_1S_4 plant was also used as the mother against pollen from BH-II plants in 3 tests not shown in the table, with negative results.

In table 20 are the results of the tests with Family BI. The plants of BI-I are fertile in all combinations, and can be given the formula S_1S_{14}. The plants of BI-II belong to the group S_1S_5. Besides the tests shown in the table, 3 other tests were made with pollen of S_1S_5, while 2 tests were

TABLE 21 1

Tests of Family BK.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLATN	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BK-I-10	BA-II-32	+	BK-II-1	BA-II-32	+
BK-I-3	BB-I-2	+	BK-II-2	BB-I-2	+
BK-I-3	BB-II-1	+	BK-II-2	BB-II-1	+
BK-I-3	BC-I-1	+	BK-II-2	BC-I-1	+
BK-I-3	BC-II-21	+	BK-II-2	BC-II-21	+
BK-I-3	BD-I-1	+	BK-II-2	BD-I-1	+
BK-I-3	BD-II-44	+	BK-II-2	BD-II-44	−
BK-I-3	BE-I-1	+	BK-II-2	BE-I-1	+
BK-I-3	BE-II-28	+	BK-II-42	BE-II-28	+
BK-I-3	BF-I-2	+	BK-II-42	BF-I-2	+
BK-I-3	BF-II-13	+	BK-II-42	BF-II-13	+
BK-I-3	BG-I-1	−	BK-II-42	BG-I-1	+
BK-I-3	BG-II-32	+	BK-II-42	BG-II-32	+
BK-I-3	BH-I-3	+	BK-II-42	BH-I-3	+
BK-I-3	BH-II-21	+	BK-II-42	BH-II-21	+
BK-I-3	BI-I-1	+	BK-II-42	BI-I-1	+
BK-I-3	BI-II-32	+	BK-II-42	BI-II-32	+
BK-I-3	BK-I-3	−	BK-II-42	BK-I-3	+
BK-I-3	BK-II-1	+	BK-II-42	BK-II-1	−
BK-I-3	BL-I-1	+	BK-II-42	BL-I-1	+
BK-I-3	BL-II-31	+	BK-II-42	BL-II-31	+
BK-I-10	S1S2	+	BK-II-1	S1S2	+
BK-I-41	S1S2	+	BK-II-43	S1S2	+
BK-I-10	S1S3	+	BK-II-1	S1S3	+
BK-I-41	S1S3	+	BK-II-43	S1S3	+
BK-I-10	S1S4	+	BK-II-1	S1S4	+
BK-I-41	S1S4	+	BK-II-43	S1S4	+
BK-I-10	S1S5	+	BK-II-1	S1S5	+
BK-I-41	S1S5	+	BK-II-43	S1S5	+
BK-I-10	S1S6	+	BK-II-1	S1S6	+
BK-I-41	S1S6	+	BK-II-43	S1S6	+
BK-I-10	S1S7	−	BK-II-1	S1S7	+
BK-I-41	S1S7	−	BK-II-43	S1S7	+

made of the reciprocal combination. All of these tests showed the matings to be incompatible. Plants of BI-II were also sterile in reciprocal combinations with the other S_1S_5 group BB-II. The other combinations were fertile.

Table 21 shows the tests made with Family BK. The plants of BK-I have the formula S_1S_7. Besides the tests shown, 3 other matings with S_1S_7 plants failed and 2 matings $S_1S_7 \times$BK-I failed. BK-I plants were also sterile to the plants of BG-I, as was to be expected. The other combina-

TABLE 22

Tests of Family BL.

TYPE I			TYPE II		
MOTHER PLANT	POLLEN PLANT	RESULT	MOTHER PLANT	POLLEN PLANT	RESULT
BL-I-2	BA-II-32	+	BL-II-27	BA-II-32	+
BL-I-2	BB-I-2	+	BL-II-4	BB-I-2	−
BL-I-2	BB-II-1	+	BL-II-4	BB-II-1	+
BL-I-2	BC-I-1	+	BL-II-4	BC-I-1	+
BL-I-2	BC-II-21	+	BL-II-4	BC-II-21	+
BL-I-2	BD-I-1	+	BL-II-4	BD-I-1	+
BL-I-2	BD-II-44	+	BL-II-4	BD-II-44	+
BL-I-2	BE-I-1	+	BL-II-4	BE-I-1	+
BL-I-2	BE-II-28	+	BL-II-4	BE-II-28	+
BL-I-2	BF-I-2	+	BL-II-4	BF-I-2	+
BL-I-2	BF-II-13	+	BL-II-4	BF-II-13	+
BL-I-2	BG-I-1	+	BL-II-4	BG-I-1	+
BL-I-2	BG-II-32	+	BL-II-4	BG-II-32	+
BL-I-2	BH-I-3	+	BL-II-4	BH-I-3	+
BL-I-2	BH-II-21	+	BL-II-4	BH-II-21	+
BL-I-2	BI-I-1	+	BL-II-4	BI-I-1	+
BL-I-1	BI-II-32	+	BL-II-4	BI-II-32	+
BL-I-1	BK-I-3	+	BL-II-4	BK-I-3	+
BL-I-1	BK-II-1	+	BL-II-4	BK-II-1	+
BL-I-1	BL-I-1	−	BL-II-4	BL-I-1	+
BL-I-1	BL-II-31	+	BL-II-4	BL-II-31	−
BL-I-2	S1S2	+	BL-II-26	S1S2	+
BL-I-25	S1S2	+	BL-II-27	S1S2	+
BL-I-2	S1S3	−	BL-II-26	S1S3	+
BL-I-25	S1S3	−	BL-II-27	S1S3	+
BL-I-2	S1S4	+	BL-II-26	S1S4	+
BL-I-25	S1S4	+	BL-II-27	S1S4	+
BL-I-2	S1S5	+	BL-II-26	S1S5	+
BL-I-25	S1S5	+	BL-II-27	S1S5	+
BL-I-2	S1S6	+	BL-II-26	S1S6	−
BL-I-25	S1S6	+	BL-II-27	S1S6	−
BL-I-2	S1S7	+	BL-II-26	S1S7	+
BL-I-25	S1S7	+	BL-II-27	S1S7	+

tions were fertile. BK-II plants were found to be fertile in all combinations except those involving BD-II. Thus, they belong to the S_1S_{10} group.

The tests of Family BL are shown in table 22. The BL-I plants were fertile in all combinations except with S_1S_3. The reciprocal combination, $S_1S_3 \times$BL-I also failed twice. The plants are therefore S_1S_3. The plants of the BL-II group have the formula S_1S_6, as shown by their incompatibility to S_1S_6 pollen. Reciprocals were also sterile. They were also sterile in reciprocal combinations to plants of BB-I (S_1S_6). All other combinations were fertile.

DISCUSSION

The original material with which the senior author began his studies on self-sterile plants some 18 years ago consisted of *Nicotiana alata grandiflora* from 4 sources (3 from seedsmen in the United States and 1 from Italy, through the UNITED STATES DEPARTMENT OF AGRICULTURE) and seed from a plant which was determined as *Nicotiana Forgetiana*. The plants of the second type grew from seed obtained from a Gray Herbarium sheet erroneously labeled *Nicotiana Clevelandii*. This plant had been sent in by a Californian botanist. It had been grown from seed obtained from Sander and Sons and had been called *Nicotiana Sanderæ*. Now, *Nicotiana Sanderæ* had been produced by crossing *N. Forgetiana* with *Nicotiana alata grandiflora*, which had produced the well-known large-flowered, many-colored hybrids. And Sander and Sons have repeatedly claimed that they did not distribute seed from the pure species *Nicotiana Forgetiana*,—a South American species which has apparently been collected but once. But since the seeds from the Gray Herbarium sheet produced a *uniform* population of plants having *small, red flowers*, corresponding perfectly with the plate (8006) for the species published in the BOTANICAL MAGAZINE, it is possible that they did indeed belong to *N. Forgetiana*. It is also possible that they were segregates from *Sanderæ* hybrids. Be that as it may, the studies on self-sterility made in this laboratory up to 1924 were made upon this so-called *Nicotiana Forgetiana*, upon *Nicotiana alata grandiflora*, and upon hybrids between the two types. Nearly all of the work was done upon the hybrids. The indications are that the original material contained several *S* factors. This conclusion may be deduced from the fact that in the earlier years cross-fertility was very high. The later experiments were upon inbred lines of this material; and therefore presumably not over 2 of the 3 *S* factors found could have come from the so-called *Nicotiana Forgetiana*.

The new material described earlier in this paper came from Sanderæ hybrids and from *Nicotiana alata grandiflora*. It was obtained from 5 different seedsmen. But although *Nicotiana alata grandiflora* was grown in this country long before the Sanderæ hybrids were produced, there is no guarantee that the material that we obtained contains a random sample of the *S* factors carried by either *Nicotiana Forgetiana* or by *Nicotiana alata grandiflora*. All that can be claimed is that the 16 plants (besides a second S_1S_4 plant) of new material investigated from a random sample of the *Sanderæ* hybrids and the *alata* hybrids now being grown in this country,—in so far as 16 plants can be a random sample of anything. These 16 plants proved to have the following genetic formulæ:- Farquhar's *alata*, S_2S_6, S_5S_7; Farquhar's *Sanderæ*, S_2S_3, S_1S_4, S_1S_5; Dreer's *alata*, S_8S_{15}, S_2S_9, S_3S_6; Dreer's *Sanderæ* S_9S_{10}, S_7S_8; Mitchell's *alata*, S_5S_6; Vaughan's *alata*, $S_{11}S_{12}$; Vaughan's *Sanderæ*, S_8S_{11}, S_4S_{13}, S_5S_{14}; and Ferry's *Sanderæ*, S_7S_{10}.

It may be seen, then, that factors S_1, S_2, and S_3, which had been isolated from our original material, were again recovered. S_1 was found only in Farquhar's *Sanderæ*; but S_2 and S_3 were found both in *Sanderæ* and in *alata*, and in plants obtained both from Farquhar and from Dreer. Of the other factors found more than once, S_4 and S_{10} were found only in *Sanderæ*, from Farquhar and Vaughan, and from Dreer and Ferry, respectively; S_6 was found only in alata, but from the 3 sources Farquhar, Dreer, and Mitchell. The remaining 4 factors that were found more than once were common to both alata and Sanderæ. Farquhar's *Sanderæ*, Mitchell's *alata*, and Vaughan's *Sanderæ* contained S_5; Farquhar's *alata*, Dreer's *Sanderæ*, and Ferry's *Sanderæ* contained S_7; Dreer's *alata* and *Sanderæ* and Vaughan's *Sanderæ* contained S_8; Dreer's *alata* and *Sanderæ* contained S_9; while Vaughan's *alata* and *Sanderæ* contained S_{11}. Thus it is evident that the *alata* hybrids and the *Sanderæ* hybrids are as similar to each other as are different samples of each type. One suspects that the *alata* plants now being grown by horticulturists are merely white-flowered segregates of the *Sanderæ* hybrids, and that all of the stocks sold by the various seedsmen are closely related; but this matter cannot be settled unless a study is made of material *known* to be unrelated to that in current circulation here in this country.

One is tempted, on the assumption that the 16 plants investigated form a random sample, to estimate the probable total number of *S* allelomorphs in the material used; but it is doubtful whether such a pastime can yield results of real value. 32 factors were determined thus:

Factors	S_1	S_2	S_3	S_4	S_5	S_6	S_7	S_8	S_9	S_{10}	S_{11}	S_{12}	S_{13}	S_{14}	S_{15}
Frequency	2	4	2	2	3	3	3	3	2	2	2	1	1	1	1

It is possible to treat this distribution as a normal frequency distribution centering on S_2, which was met 4 times. The standard deviation of this distribution is $3.5 \pm .3$; and the probable number of classes into which the variates should fall is expressed by the formula $4\sigma^2+1$, or 50. But unfortunately, there is no common-sense justification for such a calculation. Another set-up of the problem shows how far the above assumption may lead us astray. Let us assume that the number of factors in our material is exactly 15, or exactly 16, or 20, and that each factor is to be found with the same frequency. If there are exactly 15 factors, the most probable appearance of any particular factor is 2, the next most probable appearance of particular factor is 1 or 3. Actually, 2 appeared 6 times; 1 and 3 appeared 4 times each. Calculation is unnecessary. It is obvious that, with the assumption of equal frequency for all factors, it is quite probable that there are only 15 factors and highly improbable that there are more than 20 factors. But there is no good reason for making the above assumption. Indeed it is the common experience in genetics that factors are not found with equal frequency. Some are plentiful, some are rare. There is even evidence in this case that plants containing certain S factors are less viable than plants containing other S factors. And the more unequal the distribution is assumed to be, the greater the probable number of factors. The reasonable conclusion for us to draw, therefore, should run somewhat like this: other S factors may exist; but the number must be decidedly limited and the frequency so low that a further investigation of a scope humanly possible[1] could hardly be expected to add more than 4 or 5 factors to the present number.

The division of the progeny of all crosses of the type $S_xS_y \times S_1S_1$ into two approximately equal groups of plants $S_1S_x \times S_1S_y$ shows that we are dealing with mutations of a single locus. There is no evidence that factors at a second locus have a direct effect on the behavior of these self-sterile plants. It is probable, however, that, given the presence of a particular S factor, such as S_1S_1, subsidiary factors accelerate or retard pollen-tube growth in a limited fashion. That is to say, our experience leads us to believe that in a plant S_1S_2WW the pollen tube may grow faster after an

[1] One would now have to test unknown factors against 15 testers, and this work would increase with every additional factor discovered.

incompatible mating than it will in a plant S_1S_2ww. Moreover, BRIEGER[2] (1927) has reported the isolation of one such factor "*P*", apparently belonging to the same linkage group as the "*S*" factors, which accelerates the rate of pollen-tube growth where S_3 is involved.

Environmental conditions also have an effect upon pollen-tube growth. Direct evidence that such is the case has been obtained by making pollinations of a given type on certain plants kept under different conditions and studying the stained pollen tubes at various times after pollination. When plants are kept at a temperature around 10°C, the pollen tubes grow somewhat more slowly than they do at 18°C. Similarly, plants in a healthy condition or at the height of their flowering period exhibit slower pollen-tube growth after a given pollination than if they are in a poor physiological condition or are at the end of their flowering period. We believe that this conclusion holds for all types of matings, but it is easier to demonstrate when dealing with incompatible unions where pollen-tube growth is slow. Slight acceleration or retardation of the pollen tubes after a compatible mating has but little effect on time of fertilization. Fertilization occurs after a compatible mating in from 80 to 130 hours, and during the last 5 hours the tube may grow 10 mm. Since 130 hours is long before the flower would fall off if unpollinated, the slowest tubes reach the micropyle and effect fertilization; hence, indirect evidence of differential pollen-tube growth is impossible, and direct evidence is difficult to gain.

Direct evidence of differential pollen-tube growth is also difficult to obtain when two types of pollen tubes are competing and both are compatible unions,—for example, when an S_1S_1 plant is pollinated with S_2S_3 pollen. But the existing indirect genetic evidence—equality of the two classes of progeny—indicates that in all types of compatible mating, the pollen tubes grow at about the same rate. Furthermore, in a union such as $S_1S_1 \times S_1S_2$, where "incompatible" pollen tubes are competing with "compatible" pollen tubes, there is no evidence that the growth of "incompatible" pollen tubes is accelerated beyond their normal rate by the presence of the "compatible" pollen tubes.

Yet the above remarks are not the whole story, as the following argument shows. There seems to be a compensation for different style lengths of such a nature that in families segregating for style length it is not easier to obtain a given union in plants with styles 20 mm. long than it is in plants with styles 60 mm. long. In fact, the families which have shown the highest degree of self-sterility have been—although this is possibly accidental—

[2] It may be noted that BRIEGER's "*P*" factor can also be interpreted as a mutation of S^3.

families with short styled flowers. Again, unpollinated flowers usually fall off after 3 or 4 days. Flowers pollinated with incompatible pollen often remain on the plant for 10 or 12 days, although no fertilization occurs; which indicates that in incompatible matings the final stage of pollen-tube growth is not linear, as the studies of EAST and PARK (1917) indicated, but shows some retardation. And finally, by bud-pollinations, we have been able to self plants with genetic formulæ S_1S_2, S_1S_3, S_2S_4, S_2S_5, and S_2S_7, and have obtained populations of progeny indicating that the two types of pollen tubes grew at about the same rate. But bud-pollinations of S_1S_4 and S_1S_5 have never yielded seed. Thus it seems to follow that S_1 in combination with S_2 and S_3 produces pollen tubes which grow faster than when in combination with S_4 and S_5.

Thus, although in compatible unions all pollen tubes appear to grow at practically the same rate, there may be slight differences that would be detectable if accurate determinations could be made. And in incompatible unions, the pollen tubes do grow at different rates. For example, plants bearing certain *S* factors never produce seeds even after bud-pollinations or under other conditions that favor self-fertility. Plants bearing other *S* factors produce full capsules of seed after selfing in the bud. Plants bearing still other *S* factors show different degrees of pseudo-fertility under conditions favorable to fertility. If, therefore, the environmental factors affecting rate of pollen-tube growth affect all *S* factors in approximately the same degree, then plants bearing certain factors produce tubes which normally grow faster than those bearing other factors. For example, the pollen tubes bearing the factor S_4 only with the greatest difficulty can be made to grow fast enough to enable seed to be produced after a self-pollination; but pollen tubes bearing the factor S_7, which grow normally at a faster rate than those of S_4, can be shifted over into apparent fertility (our pseudo-fertility) both by favorable external conditions and by the presence of the proper heritable subsidiary factors. It is not improbable, moreover, that various other factors exist which, though they are all *S* allelomorphs, are characterized by *different* pollen-tube growth-rates that are too rapid to be shifted to a similitude with the self-sterility factors by unfavorable conditions; yet, because seed is always produced, growth-rate differences can be determined only by direct study of the pollen tube velocities. This conclusion seems probable because our factor S_{15} is a factor having a border-line pollen tube velocity. Ordinarily, full capsules of seed are produced after self-fertilization; but under conditions inhibiting pollen tube growth, the plants exhibit some self-sterility. Factor S_f, an *S* allelomorph coming from *Nicotiana Langsdorffii*, on the other hand, produces

pollen tubes which grow so rapidly that no combination of inhibiting factors will cause self-sterility.

It is natural to speculate as to the bearing of these facts, if any, on the nature of the gene, and in particular on GOLDSCHMIDT'S quantitative theory of heredity. We have isolated 16 allelomorphs of the *S* factor (including S_f). They are all point mutations, since they all behave as allelomorphs to each other and since the crossover values of 3 of them with the corolla-color factor *C* are approximately the same. It has been demonstrated that certain of these allelomorphs are characterized by pollen-tube growth-rates (after selfing) of different velocities. For instance, S_f, S_{15}, S_9, S_8, S_7, and S_4 have different normal growth rates, from high to low in that order. Now, it may be that each of these 16 allelomorphs is charactized by a pollen-tube growth-rate of velocity different from all others. It might even be possible, if these growth-rates could be determined with a high degree of accuracy and classified in descending order, to find that each differed from the other by a definite mutation-quantum expressed in velocity, as a strict interpretation of GOLDSCHMIDT'S theory would demand. Unfortunately, we cannot say that no two of these allelomorphs have identical pollen-tube growth-rates. Still more unfortunately, our experience leads us to believe that disturbing variables, both environmental and heritable, definitely prevent growth-rate determinations being made with the accuracy necessary to give us this knowledge.

On the other hand, one may assume that each *S* allelomorph differs from the next in order by a definite quantum expressed in reaction velocity and may speculate as to what conclusions follow, if any, in connection with our conception of the gene. To put the matter most simply: Does a postulate of the above type lead to the conclusion that the different velocities of the reactions directed by the various allelomorphs of a single gene are due to the presence of different quantities of the gene? Arguments in favor of such a conclusion have been presented with much vigor and clarity in the various writings of GOLDSCHMIDT. The writers have only admiration for the brilliant work of the Berlin geneticist and certainly do not wish to be numbered among those who say that his position is "neither sound genetics nor sound physiology," (GOLDSCHMIDT 1928); yet they are of the opinion that a sympathetic and receptive agnosticism in regard to his quantitative theory of gene action is at present the wisest course to take. The reasons for adopting this attitude cannot be set forth adequately in this paper; but the argument, skeletonized, runs somewhat as follows.

The gene is the unit of heredity by definition. Indirectly, we infer the genes to be rather stable physical entities arranged in an orderly manner

within the chromosomes. From calculated crossover values, we diagram their positions in the chromosomes; and we assume, from minimum known crossover values and because multiple allelomorphs show similar crossover values with specific genes in the same linkage group, that the gene physically is small. Calculations based upon minimum crossover values and chromosome size in *Drosophila melanogaster* put the bulk of the gene in the same order as that of a relatively small number of protein molecules. But it should not be forgotten that the last few points in this complex hypothesis rest upon a slender basis. Let us assume, for example, that minimal crossover values do, in fact, determine gene size, and that the minimum unit physically determinable in the fruit fly is one-fifth of one percent, or one five hundredth of the size of the chromosome. Let us assume further that there are portions of the chromosome in which five percent is the lowest crossover value. The following questions then arise: Are there no genes in this second chromosome block, which is twenty-five times the size of the other piece? Is the trouble merely that the genes in this larger piece have not been discovered? Or, more important theoretically, is the actual unit of heredity twenty-five times as large in the second case as it is in the first? We have no information on these points, but they are important to bear in mind when considering the more general aspects of the gene theory.

GOLDSCHMIDT was led to speculate on the nature of the gene from the results of his brilliant experiments on intersexes in the Gypsy moth. And he believes that in these investigations definite quantities of a gene were studied. He admits that no experimental proof has been offered to show that the sex determiners F and M are single genes; but he says that they behave like single genes, or a group of inseparable genes, and therefore the quantitative effects shown by the experiments should be interpreted as the effects of the behavior of different quantities of genes. "A quantitative relation or balance," he says, "has no meaning except in connection with the absolute quantities back of the proportion." But is this conclusion unavoidable? Our physical conception of the gene has been built up on crossover values. And on the question of sex there is no information of this precise kind. It seems valuable, therefore, to preserve the distinction; and, so long as no definite gene loci are found, to interpret sex by "gene balance."

Moreover, there is a second consideration. The gene is a biological unit, presumably different from the chemical unit, the molecule. In last analysis, however, its behavior is chemical, even though more like the working of a chemical laboratory than the reaction of a pure compound;

and it is to be hoped that chemical interpretations or descriptions may at some time become possible. Is it not advisable, then, to utilize chemical analogies where one can? It is a very simple philosophy to hold that back of quantitative behavior of hereditary units there must be a quantitative proportion of those units; but this philosophy may be more naïve than profound, for we know that in chemistry neither the type nor the velocity of a reaction can be predicted by a knowledge of the size of the molecule. It is true that the rate of a chemical reaction is proportional to the molecular concentration of the reacting substances present at a given time, and this chemical law may describe a great many of the processes of ontogeny; but it seems too simple a picture to imagine that the complex chemical laboratory of the gene is conducted solely in this manner. The facts known at present about the gene seem to require a less simple hypothesis, and we have a less simple analogy in the currently accepted hypotheses of stereo-chemistry. Even these hypotheses may be too simple, for stereo-chemistry is confined to the permutations possible in the chemical unit, the molecule. The geneticist is not so closely hedged about. Spatial relations in the larger unit, the gene, open up a wider realm of possibilities.

Both of these arguments should also be weighed, we believe, when considering the evidence from multiple allelomorphs, from triplo-, diplo-, and haplo-chromosome complexes, and from the effect of external conditions upon development. In all of these cases, it is difficult to evaluate the variables present in such a way that it is relatively certain that we are dealing with the behavior of single genes; and when this is done to the best of our ability, it is not hard to imagine a chemical mechanism at work which is quite different from that assumed by GOLDSCHMIDT.

Finally, a third argument of real value in connection with the facts of multiple allelomorphism has been suggested to us by CASTLE. When any two allelomorphs of a series are brought together in an organism, only forms containing these allelomorphs are recovered. If the quantitative theory of heredity is correct, one should expect to recover other forms. For example, let us assume that the action of the three allelomorphs S_1, S_2, S_3 is due to the presence of 1, 2, and 3 quanta of S respectively. Then the mating $S_1S_2 \times S_3S_3$ might be expected, in the second generation, to yield plants bearing factors S_1 or possibly S_4. But such is not the case.

It must be admitted that some of the evidence obtained by STURTEVANT on the bar-eye phenomena in Drosophila and some of the evidence presented by various workers on variegation appears to be interpretable most simply by hypotheses of the GOLDSCHMIDT type. Yet they may yield to other explanations. Until critical experiments are made which drive geneticists

to a definite hypothesis, therefore, it seems the part of wisdom to remain dispassionately unattached to a particular mode of explanation of these phenomena.

SUMMARY

1. Fifteen allelomorphs of the *S* factor for self-sterility have been isolated from material of the forms known as *Nicotiana alata graneiflora* and *Nicotiana Sanderæ*.

2. From the frequency distribution of the *S* allelomorphs studied, one may conclude that presumably other allelomorphs exist in this material; but they are probably few in number and presumably rare.

3. The two supposedly distinct types studied form homogeneous material, in so far as the distribution of *S* factors is concerned.

4. It is unlikely that there is a second primary locus affecting self-sterility in these forms; but subsidiary hereditary factors and certain environmental factors have noticeable effects upon the rapidity of pollen-tube growth in plants characterized by particular *S* factors.

5. The effects of subsidiary factors and of changed external conditions are not sufficient to prevent the classification of identical *S* factors by means of cross-sterility tests.

6. A number of these allelomorphs are characterized by different rates of pollen-tube growth after selfing.

7. The fact that numerous mutations have occurred in a single factor giving allelomorphs having characteristically distinct velocities of reaction, as shown by pollen-tube growth-rates, does not lead us to believe that different quantities of the *S* factor are involved.

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THE FREQUENCY OF SOMATIC MUTATION IN VARIEGATED PERICARP OF MAIZE[1]

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Some years ago (EMERSON 1922) the writer announced that in F_2 of certain crosses of variegated with colorless pericarp in maize the heterozygous individuals changed to self color more frequently than did the homozygous individuals of the same cultures.[2] No "explanation" of this phenomenon was then apparent, but later results, though still far from affording an adequate solution of the problem, have furnished at least a working hypothesis. The original unpublished paper, with minor modifications, is given below, under the heading, "Somatic mutations in heterozygous and in homozygous variegated pericarp."

In this earlier paper, variations in variegated pericarp were referred to as mutations, and it is still permissible so to designate them if the term mutation is used in a generic sense to mean any heritable change. It is even appropriate still to term these variations "gene mutations" for the genes certainly undergo changes. Since the advent of hypotheses of gene elements,[3] (EYSTER 1924, 1925, 1928) it has become apparent that the gene changes in variegated pericarp may be due merely to a sorting out of genomeres and that these changes are, therefore, possibly of quite a different nature from "ordinary" gene mutations. The writer does not care at present either to commit himself to the idea of gene elements or to reject it. He, therefore, uses the term gene mutation in the sense indicated above with no implication concerning the nature of the changes undergone by the variegation gene.

SOMATIC MUTATIONS IN HETEROZYGOUS AND IN HOMOZYGOUS VARIEGATED PERICARP

In earlier papers (EMERSON 1914, 1917), it has been shown that in races of maize with variegated[4] pericarp there occur somatic mutations from the

[1] Paper No. 160. Department of Plant Breeding, CORNELL UNIVERSITY, Ithaca, N. Y.

[2] This statement was based on data given in an unpublished paper presented before the Joint Genetics Section of the BOTANICAL SOCIETY OF AMERICA and the AMERICAN SOCIETY OF ZOOLOGISTS at the Toronto meeting, December 28, 1921.

[3] Such a hypothesis was suggested by CORRENS (1919). A somewhat different one was proposed independently by E. G. ANDERSON and M. DEMEREC in an unpublished paper presented before the Joint Genetics Sections at Toronto in 1921. Later, EYSTER outlined in detail a similar hypothesis.

recessive variegated type to the dominant self colored type. The areas affected vary from a minute part of a single seed to an entire ear or to all the ears of a plant. Two types of somatic mutations of different appearance, but presumably of the same fundamental nature, have been recognized. One, the dark-crown type, is not inherited, while the other, the self colored type, has an even chance of being inherited.[5] Non-mutated areas remain colorless. Fundamentally, therefore, variegated races differ from white ones in that they mutate somatically to the self colored condition with considerable frequency while white races, so far as observed, do not so mutate. Likewise light and dark variegated races differ from each other mainly in the frequency of their somatic mutation.

Since the gene for white does not mutate, either when duplex WW,[6] or simplex, WV, and since a single mutation affects only one of the duplex genes, VV, in homozygous variegated maize, it should follow, as pointed out in an earlier paper (EMERSON 1917), that somatic mutation will occur about twice as frequently in homozygous, VV, as in heterozygous, VW, material. This expectation is based on the assumption that the mutability of the variegation gene is uninfluenced by its allelomorphic mate or by anything associated with it.

Variegated maize pericarp is unusually favorable for a comparison of the relative mutability of homozygous and of heterozygous material. The change to self color occurs with a frequency that makes quantitative studies readily possible. The self-color mutation is dominant to variegation. Obviously this is essential to the study, for otherwise the mutation could not be expressed in homozygous variegated material. The existence of a third allelomorph that is recessive to variegation, such as white, is equally essential for otherwise heterozygous variegation would be masked by the dominant self color associated with it. A further feature of the maize material, which, if not essential, is at least of great advantage, is the possibility of distinguishing homozygous from heterozygous variegated ears without the necessity of making progeny tests. The variegated strains used in these investigations have variegated cobs as well as variegated kernels. When such strains are crossed with ones having white kernels and

[4] The writer has dealt only with the so-called "calico" variegation, not with a somewhat different type known as "mosaic" (HAYES 1917, EYSTER 1925).

[5] The writer had assumed that the dark-crown type is epidermal and the self colored type sub-epidermal in origin, but RANDOLPH (1926) has shown this assumption to be incorrect particularly with respect to the coloration at the crown of the kernel.

[6] The factor pair for pericarp color is usually designated by the sumbols P p and the several allelomorphs by superscripts. For the sake of simplicity the latter alone are here used, P being omitted. For an account of the allelomorphs of the pericarp gene, see ANDERSON (1924).

red cobs, the F_1 ears have variegated kernels and red cobs. In F_2 there occur three types in the relation of one with white kernels and red cobs, two with variegated kernels and red cobs, and one with variegated kernels and variegated cobs. The variegated ears with red cobs are always heterozygous, *VW*, while those with variegated cobs are homozygous, *VV*, for pericarp color.

The procedure suggested by the considerations noted above was followed in the tests to be reported here. Strains of maize with variegated pericarp and cobs were crossed with red cobbed whites and the F_1 plants were self-pollinated. The variegated ears of each F_2 progeny were first separated into two lots, one with self red and the other with variegated cobs. Each lot was then classified into color grades from very light variegation, grade 1, in which most kernels are white, only a few showing narrow red stripes, to very dark variegation, grade 7, in which most kernels show numerous fine red stripes. Next, each ear was examined separately, the approximate total number of kernels noted, and the numbers of self colored and partly self colored kernels determined. In these determinations, narrow red stripes were disregarded, no kernel being classed as partly self colored unless it had a broad self colored stripe involving perhaps one tenth of the area of the kernel. Each group of self colored kernels was noted separately and the number of kernels in it recorded. The same procedure was followed in noting dark-crown variations except that no account was taken of changes affecting less than an entire kernel.[7]

In all, fourteen F_2 progenies with 570 ears and approximately 240,000 kernels were examined. The number of groups of self colored and partly self colored kernels of homozygous, *VV*, and of heterozygous, *VW*, ears are recorded in table 1. The data are expressed as numbers of groups (mutations) per 1000 kernels and are so arranged that class centers for number of kernels per group are doubled for each succeeding class. The first class includes all kernels from about one tenth to almost entirely self colored.

It is clear from the data given in table 1, that, contrary to expectation, heterozygous variegated pericarp, *VW*, instead of mutating about one half as frequently as homozygous, *VV*, material, actually mutated more frequently. This is particularly noticeable for mutations affecting a single kernel or less. On the whole the single variegation gene of heterozygous ears mutated 1.42 times as frequently as the two variegated genes of homozygous ears.

[7] For making most of these counts, the writer is indebted to M. DEMEREC and FRED DENNIS.

TABLE 1

Number of self-color mutations per 1000 kernels in homozygous and in heterozygous variegated ears.

GENOTYPE	CLASS CENTERS FOR NUMBER OF KERNELS AFFECTED											TOTAL
	1/2	1	2	4	8	16	32	64	128	256	512	
VV	17.16	3.93	1.23	.543	.095	.027	.014	..	.014	..	.014	23.03
VW	24.13	5.95	1.97	.501	.085	.036	.006	.006	.018	.024	.012	32.74
Ratio *VW*:*VV*	1.41	1.51	1.60	.92	.89	1.33	.43	..	1.29	..	.86	1.42

TABLE 2

Number of dark-crown mutations per 1000 kernels in homozyous and in heterozygous variegated ears.

GENOTYPE	CLASS CENTERS FOR NUMBER OF KERNELS AFFECTED										TOTAL
	1	2	4	8	16	32	64	128	256	512	
VV	3.85	.86	.543	.162	.095	.014	.014	.014	.014	..	5.57
VW	4.78	1.11	.851	.296	.163	.066	.006	.018	.012	.054	7.36
Ratio *VW*:*VV*	1.24	1.29	1.57	1.83	1.72	4.71	.43	1.29	.86	..	1.32

Data obtained from counts of dark-crown kernels of the same F_2 progenies are given in table 2.

Mutations resulting in dark-crown kernels occurred on the whole 1.32 times as frequently in heterozygous as in homozygous material, the difference being practically the same as was found for self-color mutations. There seems, therefore, no escape from the conclusion that the single variegation gene of *VW* material had a mutability of about 2.7 times that of either one of the two variegation genes of *VV* material.

The differences noted above are even more strikingly shown when light variegated strains alone are considered. Of the fourteen F_2 progenies from which the records given in tables 1 and 2 were obtained, five came from crosses of red cobbed whites with light variegated types of maize. They included 259 ears and approximately 114,000 kernels. The data from these progenies are given in table 3.

In these light variegated strains, as seen from table 3, self-colored mutations occurred about 3 times and dark-crown mutations 2.3 times as frequently in heterozygous as in homozygous ears, an average of 2.64 times as frequently in the one as in the other lot. This, the writer is inclined to believe, can mean nothing other than that the single variegation gene of *VW* ears had a mutability of more than five times that of either one of the two variegation genes in *VV* ears.

In the nine F_2 progenies from crosses of dark variegated strains with red cobbed whites, the number of somatic mutations of both the self-colored and the dark-crown types together was 1.1 times as great in heterozygous as in homozygous ears. Even here the mutability of the one *V* gene of *VW* ears must, it would seem, have been at least twice as great as that of either one of the two *V* genes in *VV* ears.

So far no account has been taken of the somatic mutations that occur so late in development that they result merely in narrow streaks of red. The relatively great frequency of occurrence of these fine red stripes makes it difficult if not impossible to count them. (See ANDERSON and EYSTER 1928) They were, however, evaluated fairly accurately as noted earlier in this account, by classifying the F_2 ears into color grades from very light, grade 1, to very dark, grade 7, the several grades being dependent largely on the relative number of fine red stripes on the seeds. A total of 368 ears, one ear per plant, from seven of the F_2 progenies, were thus graded. A summary of the data is given in table 4.

The mean color grade of the heterozygous ears was 1.27 grade higher than that of the homozygous ears, a difference of over twelve times its probable error. Calculated by PEARSON'S (1908) formula for comparing

TABLE 3

Number of self-color and dark-crown mutations per 1000 kernels in homozygous and in heterozygous light variegated types of maize.

GENOTYPE	CLASS CENTERS FOR NUMBER OF KERNELS AFFECTED											TOTAL
	1/2	1	2	4	8	16	32	64	128	256	512	
SELF-COLOR MUTATIONS												
VV	7.65	1.06	.287	.086	..	..	.029	..	..	..	..	9.11
VW	21.31	4.78	.629	.390	.063	.038	..	..	..	.013	.013	27.24
Ratio *VW*:*VV*	2.79	4.51	2.19	4.53	..	..	..	..	..	..	..	2.99
DARK-CROWN MUTATIONS												
VV	..	1.67	.316	.201	..	..	..	..	..	..	..	2.19
VW	..	3.22	.893	.578	.176	.038	.050	..	.025	.013	.025	5.02
Ratio *VW*:*VV*	..	1.93	2.83	2.88	..	..	..	..	..	..	..	2.29

two independent distributions, $\chi^2 = 67.59$. Such a value of χ^2, where $n' = 7$, leaves no doubt that the two distributions in question are significantly different.[8] It follows, therefore, that the difference in frequency of somatic mutation between *VV* and *VW* material is much the same when determined by color grades based on fine red stripes as when determined from the number of groups of self colored and dark-crown kernels.

TABLE 4

Number of ears of various color grades in homozygous and in heterozygous variegated maize.

GENOTYPE	VARIEGATION GRADES							TOTAL	MEAN GRADE
	1	2	3	4	5	6	7		
VV	7	37	19	24	17	4	..	108	3.18
VW	..	29	48	39	73	64	7	260	4.45
Difference	..	..	..	..	..	..	..	...	1.27
Ratio *VW*:*VV*	..	..	..	..	..	..	..		1.40

What appears to be behavior similar to that noted above for maize was reported by CORRENS (1903) for Mirabilis. Pink, yellow, and pale yellow flowered races of Mirabilis were crossed with what was at the time regarded as a white flowered race. The F_1 plants had strongly variegated flowers, about one third of them showing some wholly self colored flowers and a few having entire branches with such flowers. Later (CORRENS 1904) it was observed that the supposedly white flowered race used in these crosses produced a few flowers with minute red streaks. Evidently it was an extremely light variegated type. No variegated flowers were observed in any of the pink or yellow races with which it was crossed nor were any such seen in the progenies of intercrosses between these pink and yellow races. CORRENS interpreted these results as due to the interaction of factors brought into the cross from the two parents, factors that were wholly latent in the pink and yellow races and almost wholly so in the so-called white race. It appears, therefore, that the mutability of the gene for

[8] One is perhaps not warranted in using the probable error as calculated by the usual formula $0.6745\delta/\sqrt{n}$ from arrays so unlike a normal frequency distribution as these are. Pearson's formula, $\chi^2 = S_{1s}\left\{\frac{NN'\left\{\frac{f_p}{N} - \frac{f_{p'}}{N'}\right\}^2}{f_p + f_{p'}}\right\}$, has been used in place of or together with the formula for the probable error of the mean in determining the probable significance of differences between the frequency distributions reported in this paper.

variegated flowers in Mirabilis is increased in crosses with non-variegated races much as is the gene for variegated pericarp in maize.

It seems unlikely that the behavior noted in maize can be explained by the assumption of an interaction of independently inherited modifying factors furnished by the two parents. If the mutability of the variegation gene is influenced in any such way, it should be possible to find crosses that would not produce the effects so far observed. To explain thus the behavior noted in maize, the postulated modifying factor must be the allelomorph of the variegation gene or some factor or factors linked with it. It must be remembered in this connection that in maize the comparison was made between homozygous and heterozygous ears of the same F_2 progenies grown from self pollinated F_1 heterozygotes—a circumstance that would afford abundant opportunity for recombinations of independently inherited modifying factors.

DIFFERENTIAL EFFECTS OF VARIOUS WHITE RACES ON THE MUTABILITY OF THE VARIEGATION GENE IN CROSSES

The suggestion offered in the last paragraph of the earlier paper, as quoted above, that, if the mutability of the variegation gene is influenced by factors carried by the white parent of heterozygous ears, it should be possible to find white strains which would have no such effect in crosses, has been tested in later studies.

In 1923 several white races of maize were crossed with pollen of three individuals of a culture of variegated maize. The white races were selected from diverse types, such as dent, flint, flour, and sweet varieties or crosses. The three plants, from which pollen was used in the crosses, were homozygous for variegation, *VV*, but were F_2's of a cross between a very light variegated type and a dark variegated type. In order to be sure that the pollen used on the several white races was as uniform as possible, one day's production of pollen from each variegated plant was divided and applied at once to the silks of the several white races. Pollen of these three variegated plants was used also on other variegated cultures, which were segregating, producing white, homozygous variegated and heterozygous variegated ears. Finally, each of the three pollen parents of these crosses was selfed.

F_1 progenies of these crosses and progenies from the self pollinations were grown in 1924 and duplicate cultures of some of them in 1927.

Since the earlier work had indicated that differences in frequency of mutation could be determined with fair accuracy by grading the ears into classes from very light variegated, grade 1, or no variegation, grade 0, to very dark variegated, grade 7, and since this method is much less labori-

ous than the counting of self colored kernels (compare tables 1 and 4), the grading method alone was used in the later work. Extreme accuracy is not claimed for this method. In fact, it is likely that most any sample of ears would be graded somewhat differently at different times. To test this the writer reclassified three lots of ears one month after they had been graded the first time, and without referring to the earlier records. The results are given in table 5.

TABLE 5

Comparison of independent classifications of identical lots of variegated ears.

CULTURE	CLASSIFICATION	DISTRIBUTION OF EARS OF THE SEVERAL VARIEGATION GRADES							TOTAL NUMBER OF EARS	MEAN GRADE
		1	2	3	4	5	6	7		
1	First			21	18	10	8	3	60	4.23
	Second			21	20	8	8	3	60	4.20
2	First				8	9	19	13	49	5.76
	Second				9	8	23	9	49	5.65
3	First	106	35	4					145	1.30
	Second	97	44	4					145	1.36

As might well be expected there was less close agreement between the grading of lots grown and classified in 1924 and the duplicate lots grown in 1927. Since, fortunately, the 1924 lots had been preserved and were re-examined immediately after the 1927 lots had been classified, relatively little of the observed difference between the two lots as finally recorded is to be ascribed to personal errors in grading. The differences, as will be shown later, were not greater than might be expected from small random samples of the same lots.

The results obtained from the 1924 cultures, together with those from such duplicates as were grown in 1927, are given in table 6.

Although there are differences in the frequency distribution of variegation grades between duplicate cultures grown in 1924 and 1927, on the whole the differences are surprisingly small. In no case is the difference in mean grade between the two lots as much as three times its probable error, and in only one case does it approach closely that magnitude. And in no case were the frequency distributions significantly different as determined by PEARSON'S (1908) formula. Duplicate cultures may, therefore, be combined and treated as one lot.

A strikingly different situation from the above is presented by the fre-

TABLE 6

Number of individuals of various grades of variegation in F_1 of crosses of variegated maize with white races from diverse sources.

PARENT CULTURE NUMBERS		F_1 PROGENY									
VARIEGATED	WHITE	YEAR GROWN	VARIEGATION GRADES							TOTAL	MEAN GRADE
			1	2	3	4	5	6	7		
13358–3	..	1924	17	15						32	1.47
	13363-2	1924		1	2	17	24			44	4.45
		1927		1	7	40	36	1		85	4.34
	13369-3	1924			2	18	5			25	4.12
		1927			4	62	6			72	4.03
	13371-1	1924			3	23	2			28	3.96
	13372-1	1924			12	16	3	1		32	3.78
	13367-1	1924	1		11	46				58	3.76
	13366-1	1924			10	23	1			34	3.74
	-5	1924			16	32	2			50	3.72
13358-5	..	1924	7	6	6	1		2		22	2.41
		1927	33	25	23	7	5	3		96	2.32
	13363-3	1924			7	7	7			21	4.00
		1927			21	18	10	8	3	60	4.23
	13369-4	1924	2	5	8	3	5	4	7	34	4.29
		1927	6	8	11	7	5	9	6	52	3.92
	13371-2	1924		5	11	21	12	3		52	3.94
	13372-2	1924		3	10		11			24	3.79
	13367-2	1924		3	10	14	5	1		33	3.73
	13366-2	1924		5	16	13	8			42	3.57
13358-6	..	1924			7	3	1	5		16	4.25
		1927		1	3	5	4	3		16	4.31
	13363-1	1924				7	7	11	2	27	5.30
		1927				8	9	19	13	49	5.76
	13372-5	1924		1	2	6	13	2		24	4.54
	13367-4	1924		1	4	10	19	3	1	38	4.58

quency distributions and mean grades of the several F_1 progenies of either variegated parent crossed with the different white types. For ready comparison the mean grades of all crosses are summarized in table 7.

TABLE 7

Mean grades of variegation in F_1 of crosses between homozygous variegated plants and different white races of maize.

SEED PARENTS	VARIEGATED POLLEN PARENTS		
	13358-3	13358-5	13358-6
13358-3	1.47		
-5		2.34	
-6			4.28
13363-2	4.38		
-3		4.17	
-1			5.59
13369-3	4.05		
-4		4.07	
13371-1	3.96		
-2		3.94	
13372-1	3.78		
-2		3.79	
-5			4.54
13367-1	3.76		
-2		3.73	
-4			4.58
13366-1	3.74		
-5	3.72		
-2		3.57	

Plant 3 (culture 13358) produced a very light variegated ear, grade 1, and its progeny from selfing had a mean grade of 1.47. When this plant was crossed onto a plant of culture 13363, the mean grade of its F_1 progeny was 4.38. Crosses with other white varieties gave lower F_1 grades, the differences in some cases, however, not being statistically significant. The lowest F_1 grades of the crosses with pure colorless varieties was 3.74 and 3.72 for two crosses on plants of culture 13366. The difference in mean grade between the crosses with 13363 and 13366 is 0.65, which is more than ten times the probable error of the difference. The frequency distributions

of these two cultures are so unlike that χ^2 calculated from them has a value of 72.6.

Similar differences are shown between the F_1 grades of crosses of the other two variegated plants, individuals 5 and 6 of culture 13358. Plant 5 had an ear of slightly darker variegation, grade 2, than plant 3 and its progeny from selfing was of correspondingly higher grade, 2.34. Plant 6 was medium variegated, grade 5, and its progeny from selfing had a mean grade of 4.28. The progeny grades of crosses of these two variegated plants with the several white varieties show the same trend as is exhibited by the crosses of variegated plant 3. Thus the progeny of a cross of plant 5 on 13363 had a mean grade of 4.17 while a cross of plant 5 on 13366 produced a progeny of mean grade 3.57. These facts strengthen materially the conclusion that different colorless varieties influence differently the mutability of the variegation gene in crosses.

In addition to the crosses with white varieties of diverse types discussed above, the same three variegated plants of culture 13358 were crossed on seven plants grown from seed of a self pollinated variegated plant, which was heterozygous for variegation because of an earlier cross with a red cobbed white. The selfed ear from which these seven plants were grown had a red cob and was light variegated, grade 2. None of the seven plants used as seed parents of the crosses with the three homozygous variegated plants of culture 13358 was selfed so that what their progenies would have been is unknown. The grade of variegation of each of the seven crossed ears, however, was noted, and these grades are given in table 8, together with the detailed results of the crosses.

Before a discussion of these results is given, the origin of the stock, culture 13360, in which the seven crossed ears were produced may well be noted. This stock came from a long line of pedigree breeding tracing back in some ancestral lines for 18 generations of cross and self pollinations. No less than three distinct variegated strains and 15 white strains were combined in its ancestry. In the near ancestry of 13360 there were two generations from selfing of homozygous plants all of low grade variegation, as follows. Culture 9318 had a mean grade of 2.0. From a selfed ear of grade 1 of this lot, there was grown culture 10057, the mean grade of which was 1.0. A selfed ear of this lot of grade 0 (one on which no grain with any red stripe could be found) produced culture 11311 with a mean grade of 0.82. An ear of grade 1 of this lot pollinated by a homozygous red cobbed white of complex ancestry produced culture 12152 with a mean variegation grade of 4.25. A selfed ear of grade 2 of this lot produced culture 13360. Two of the seven ears of 13360 that were crossed by one or other

of the three variegated plants of 13358 were homozygous red cobbed whites, one was a homozygous variegated cobbed variegate, and four were heterozygous red cobbed variegates.

The F_1 progenies of these seven crosses are given in table 8, together

TABLE 8

Number of individuals of various grades of variegation in F_1 of crosses of homozygous variegated plants with the progeny of a heterozygous variegated plant.

POLLEN PARENT CULTURE NUMBER	SEED PARENT			F_1 PROGENY										
	CULTURE NUMBER	GENOTYPE	GRADE	GENOTYPE	YEAR GROWN	VARIEGATION GRADE								TOTAL	MEAN GRADE
						0	1	2	3	4	5	6	7		
13358-3	Selfed	*VV*	1	*VV*	1924		17	15						32	1.47
	13360-8	*WW*	0	*VW*	1924		7	17	18	8				50	2.54
					1927		17	20	36	10				83	2.47
	-3	*VW*	1	*VW*	1924	1	6	30	1	1				39	1.87
				VV	1924	1	33	5	1	1				41	1.22
	-4	*VW*	1	*VW*	1924	1	31	14		1				47	1.34
					1927		32	31	3					66	1.56
				VV	1924	1	49	1						51	1.00
					1927		74	4	1					79	1.08
13358-5	Selfed	*VV*	2	*VV*	1924		7	6	6	1		2		22	2.41
					1927		33	25	23	7	5	3		96	2.32
	13360-10	*WW*	0	*VW*	1924	1		5	12	8	9	1		36	3.58
	-7	*VW*	3	*VW*	1924		4	4	6	12	1	2		29	3.28
					1927		11	7	7	13	3		4	45	3.13
				VV	1924	1	2	4	8	3	1			19	2.68
					1927		15	10	6	3	4	3	1	42	2.62
	-5	*VV*	1	*VV*	1924	2	13	13	3		1			32	1.66
13358-6	Selfed	*VV*	5	*VV*	1924				7	3	1	5		16	4.25
					1927			1	3	5	4	3		16	4.31
	13360-13	*VW*	3	*VW*	1924	1	1		5	17	5	5		34	4.09
					1927	2	1	9	8	19	6	11	8	64	4.23
				VV	1924		6	6	6	7	5	1		31	3.06
					1927		4	18	11	7	11	8		59	3.46

with the grades of the progenies of the selfed pollen parents of the crosses.

Here, again, there are no statistically significant differences in mean grade between the duplicate cultures grown in 1924 and 1927. The mean grades of all these progenies, with duplicate cultures combined, are summarized in table 9.

TABLE 9

Mean grades of variegation in F_1 of crosses between homozygous variegated plants and the progeny of a heterozygous variegated plant.

SEED PARENTS				VARIEGATED POLLEN PARENTS		
CULTURE NUMBER	GRADE	GENOTYPE	♀ GAMETE	13358-3	13358-5	13358-6
13358-3	1	*VV*	*V*	1.47		
-5	2	*VV*	*V*		2.34	
-6	5	*VV*	*V*			4.28
13360-8	0	*WW*	*W*	2.50		
-10	0	*WW*	*W*		3.58	
-5	1	*VV*	*V*		1.66	
-3	1	*VW*	*W*	1.87		
			V	1.22		
-4	1	*VW*	*W*	1.47		
			V	1.05		
-7	3	*VW*	*W*		3.19	
			V		2.64	
-13	3	*VW*	*W*			r.18
			V			3.32

The two red cobbed white plants, 8 and 10, of culture 13360 when crossed by homozygous variegated plants gave progenies with a higher mean grade of variegation than did the self pollinted pollen parents of these crosses. But the mean grades of these crosses were materially lower than crosses of the same pollen parents on any of the white races as recorded in tables 6 and 7. It is perhaps a plausible suggestion that the very low grade variegation of the near ancestors of these two whites had in some way lessened their ability to increase the mutability of the variegation gene of the low grade pollen parents.

A single homozygous very light variegated, grade 1, plant 5, of culture 13360, crossed by plant 5 of culture 13358 produced an F_1 with a mean grade of variegation of 1.66. The pollen parent of this cross had a varie-

gation grade of 2 and its progeny from selfing a mean grade of 2.34. Evidently this very low grade seed parent was able to reduce the grade of variegation of the pollen parent.

Two heterozygous (red cobbed) variegated plants, 3 and 4, of culture 13360 crossed by plant 3 of culture 13358 gave progenies that were not far different in grade from the progeny of the selfed pollen parent. The fact that these two heterozygous variegated plants had red cobs made it possible to separate their F_1 progenies into two lots, one with red cobs and the other with variegated cobs. The variegated cobbed lots must have carried the variegation genes of the heterozygous seed parents and have been homozygous variegated, *VV*. Likewise the red cobbed lots must have carried the white genes of the heterozygous seed parents and therefore must themselves have been heterozygous, *VW*. The two heterozygous seed parents had very light variegated ears, grade 1, and the pollen parent also a light variegated ear, grade 1. The progeny of the selfed pollen parent had a mean grade of 1.47. The mean grades of the homozygous ears (variegated cobs) of the F_1 progenies were 1.22 and 1.05. Apparently the very low grade variegation genes of the seed parents, or something carried in the same chromosome with them, reduced, or certainly did not increase, the mutability of the variegation gene of the pollen parent.

The heterozygous ears (red cobbed)of these same F_1 cultures had mean grades of 1.87 and 1.47 respectively. The first of these mean grades is significantly higher than that of the selfed progeny of the pollen parent, 1.47; the second is identical with it. These heterozygous progenies are to be regarded as quite the equivalent of F_1 progenies of pure white races crossed by variegated plants since pure white races could have been readily established from the seed parents had they been selfed. Evidently, therefore, potential white types have been found which do not increase the grade of variegation in crosses above that of the variegated parent.

Another heterozygous variegated ear of culture 13360, individual 7, was crossed by plant 5 of culture 13358. In this cross the mean grade of the homozygous ears was somewhat, though not significantly, higher than that of the pollen parent's selfed progeny. Here the grade of the ears of the seed parent was 3. The heterozygous ears of this cross had a mean grade of 3.19 which is significantly higher than that of the pollen parent's selfed progeny, 2.34.

Finally, a heterozygous plant, 13, of culture 13360, with an ear of grade 3, crossed by plant 6 of culture 13358, gave an F_1 progeny the homozygous variegated ears of which were of significantly lower grade, 3.32, than those of the pollen parent's selfed progeny, 4.28. The heterozygous

ears of the same F_1 culture were of slightly, though not significantly, lower grade, 4.18, than that of the pollen parent's selfed progeny. Here again is involved a potential white strain which did not raise the grade of variegation of a cross above that of the variegated parent.

It must be remembered in this connection, that the assumption on which this study was based is that a homozygous variegated ear, being duplex for the variegation gene, *VV*, should have a much higher grade of variegation than one heterozygous for the same gene and therefore simplex for variegation, *VW*. From this standpoint, no white race, or potential white race, has been found that does not increase materially the grade of variegation in crosses, over that expected.

RECIPROCAL CROSSES OF VARIEGATED AND OF VARIEGATED AND WHITE PARENTS

The writer is quite unable—perhaps from lack of sufficiently keen imagination—to see how the mere fact of heterozygosity could account for the results here reported. Without the disturbing effects of other genes, heterozygotes normally exhibit complete dominance of one allelomorph over the other, or various degrees of partial dominance, or even no dominance, resulting in an almost exactly intermediate condition. Heterozygotes exhibiting characters unlike those of either parent or parental characters in an intensified form, so far as they have been carefully analyzed, have been shown to have received from one or both parents modifying or complementary genes which were responsible for the unexpected results. Variegation, however, though a wide-spread phenomenon, at least in the plant kingdom, may well be unlike "ordinary" characters, as indeed the gene-element hypothesis would have us believe.

It is conceivable that an effect ascribed to heterozygosity might be due to a peculiar reaction of chromosomes or genes of the sperm with the strange cytoplasm of the egg. It should be mentioned in this connection that culture 13360, which gave such strikingly different results from those obtained from various white strains crossed by the same variegated plants, was closely related to culture 13358 which furnished the pollen parents of all these crosses. As has been noted, culture 13360 was an F_2 of a cross of a red cobbed white with a plant of an inbred strain of very low grade variegation, 11311–5. Culture 13358 was an F_2 of a cross of the same low grade variegated plant, 11311–5, with a plant of an inbred strain of high grade variegation. It might be argued, therefore, that the cytoplasm of culture 13360 was not very different from that to which the chromosomes of culture 13358 were accustomed.

Reciprocal crosses should throw some light on such a problem as this. Detailed records of grades of variegation of reciprocal crosses are given in table 10.

TABLE 10

Number of individuals of various grades of variegation in F_1 of reciprocal crosses.

SEED PARENT			POLLEN PARENT			F_1 PROGENY							MEAN GRADE
CULTURE NUMBER	GENOTYPE	GRADE	CULTURE NUMBER	GENOTYPE	GRADE	VARIEGATION GRADES						TOTAL	
						1	2	3	4	5	6		
11311-5	*VV*	1	11312-1	*VV*	6		15	9	7	5	2	38	3.21
11312-1	*VV*	6	11311-6	*VV*	1		10	12	7	5	1	35	3.29
17434-15	*WW*	0	17435-1	*VV*	1	1	21	42	16			80	2.91
17435-1	*VV*	1	17434-15	*WW*	0		7	17	6			30	2.97
17435-1	*VV*	1	17441-2	*VV*	6		6	14	25	13	2	60	3.85
17441-2	*VV*	6	17435-1	*VV*	1		2	13	47	20	2	84	4.08
17435-5	*VV*	1	17441-7	*VV*	6	1	6	10	9	5		31	3.35
17441-7	*VV*	6	17435-5	*VV*	1		7	15	5	7		34	3.35
17820-2	*VV*	1	17826-3	*WW*	0		1	2	31	6	1	41	4.10
17826-3	*WW*	0	17820-2	*VV*	1				36	7		43	4.16

Of the five pairs of reciprocal crosses, records of which are given in table 10, there is no appreciable difference between the two members of any pair either in distribution of grades or in mean grades. Of the first pair, culture 11312 is represented by plant 1 in both the direct and the reciprocal crosses, but culture 11311 is represented by plant 5 in one cross and plant 6 in the other. In all other cases the same individuals are involved in the reciprocal crosses. Culture 11311 came from two generations of selfing and selection for low grade variegation and its mean grade was 0.82. Culture 11312 came from four generations of selfing and selection for high grade variegation and its mean grade was 4.52. The two cultures were relatively unrelated, having only five common ancestors in sixteen generations, the nearest common ancestor being ten generations removed.

The parents of the next pair recorded in table 10 were, so far as known, quite unrelated. Culture 17435 traces back five generations to culture 11311, while culture 17434 was obtained from Dr. LINDSTROM of Ames, Iowa. The plant of the latter culture used in the crosses was a heterozygous

red cobbed white from a cross of a red cobbed white with a variegated strain, out-crossed with a white cobbed white.

The next two pairs of reciprocal crosses shown in table 10 involved culture 17435, used in the above cross, and culture 17441. Both were homozygous variegated and closely related to each other and to the parents of the first pair of reciprocals of table 10. One of the lines, however, had been selected for high grade and the other for low grade variegation, as indicated by the grade numbers in parentheses after the culture numbers in the pedigree chart below.

$$17441\left\{\begin{matrix}15148\text{–}1(6)\\ \\ 15148\text{–}4(6)\end{matrix}\right\}14600\text{–}4(7)\leftarrow 13352\text{–}6(6)\leftarrow 12152\text{–}8(6)\left\{\begin{matrix}11311\text{–}5(1)\\ \\ 11318\text{–}2(0)\end{matrix}\right.$$

$$17435\leftarrow 15141\text{–}1(1)\leftarrow 14591\text{–}10(1)\left\{\begin{matrix}13360\text{–}4(1)\leftarrow 12152\text{–}2(2)\left\{\begin{matrix}11311\text{–}5(1)\\ \\ 11318\text{–}2(0)\end{matrix}\right.\\ \\ 13358\text{–}3(1)\leftarrow 12149\text{–}5(3)\left\{\begin{matrix}11311\text{–}5(1)\\ \\ 11312\text{–}1(6)\end{matrix}\right.\end{matrix}\right.$$

Culture 17441 had a mean grade of variegation of 5.75 and culture 17435 a mean grade of 1.00. Although both cultures were of so nearly the same ancestry, they differed markedly, not only in variegation grade, but in other respects, the plants of culture 17441 having only single stalks with one ear, while those of culture 17435 were tillered and had from three to five ears per plant.

The last pair of reciprocals compared in table 10 involve quite unrelated stocks. Culture 17820 was the progeny of 17435–1 of the pedigree chart given above. Its mean grade of variegation was 1.09. Culture 17826 was a red cobbed white strain which had been inbred by selfing for seven generations.

The results given in table 10, involving unrelated cultures as well as somewhat closely related ones, and including reciprocal crosses between homozygous variegates of very different grade as well as between variegates and whites, indicate clearly that reciprocal crosses are practically identical with respect to grades of variegation. This would seem to indicate that the reaction of sperm chromosomes to unaccustomed cytoplasm is not a factor of importance in influencing the mutability of the variegation gene in crosses.

THE HYPOTHESIS OF MODIFYING GENES

In the writer's opinion the most plausible interpretation of the results reported in this paper is that a gene, or perhaps more than one, at a locus other than that of the variegation gene and its allelomorphs but in the same chromosome, influences the mutability of the variegation gene, *V*. Such a modifying gene, if any exists, can not have its locus in a non-homologous chromosome, for then the chances for reassortment between chromosomes is such that in an F_2 culture the heterozygous ears, *VW*, should not have a higher grade of variegation than the homozygous ones, *VV*, as in fact they do have (table 4).

If an allelomorph of the variegation gene, such as *W-W*, white cobbed white, or *W-R*, red cobbed white, is itself responsible in crosses for the increase in intensity of variegation over that of the variegated parent, the change in the effect of this white gene from association with a low grade variegation gene, as in culture 13360, discussed above, must, it would seem, be ascribed to a direct contamination of one allelomorph by another. This is, perhaps, not beyond the bounds of possibility if the variegation gene is not a simple unit but rather composed of distinct gene elements, which might conceivably be transferred from one allelomorph to the other at synapsis. But the writer is wholly unable to devise a consistent working hypothesis to account for his results on any such assumption.

On the assumption that there exists a gene, or perhaps more than one, linked with the variegation gene and capable of modifying its mutability, results such as those derived from culture 13360 are readily interpreted on the basis of ordinary crossing over. This hypothesis of modifying genes is, at the present stage of our knowledge, not without value, for it should be possible, unless such genes are too numerous, to demonstrate its correctness or incorrectness. This the writer is, of course, attempting to do by introducing into certain variegated stocks other well known genes of the linkage group to which the variegation gene and its allelomorphs belong. That other genes modify the behavior of a mutable gene in *Drosophila virilis* has been demonstrated by DEMEREC (1928).

It is difficult for the writer to think of variegation in terms of dominance and recessiveness of variegation genes of high or low grade. His conception of the difference between low grade and high grade variegation is merely that, in the one case, mutations from white to red occur less frequently than in the other. Or, if the hypothesis of gene elements is preferred, it is a matter of the relative rapidity of the sorting out of gene elements, dependent in turn probably on the particular combination of gene

elements originally present It is doubtless conceivable, though in the writer's opinion hardly probable, that the presence in a somatic cell of a frequently changing (high grade variegation) gene could activate its less frequently changing (low grade) allelomorph, for, in that case, one must suppose also that a white gene, though mutating rarely if at all, can none the less activate its low grade variegation mate. If, however, rate of mutation of the gene, or of sorting out of its elements, is influenced by a distinct gene which can be carried in a non-variegated race, this gene of a white race might be at least partially dominant over its allelomorph from a low grade variegation stock and thereby raise the variegation grade in crosses of low grade variegation with white.

The data in table 10 may have some bearing on the question of dominance either of the variegation gene itself or of an associated gene that influences the rate of change of the variegation gene. Unfortunately none of the individual plants that were used in the reciprocal crosses reported in table 10 was selfed, so that what its progeny would have been can not be known. But the mean grades of the cultures in which these plants occurred afford some basis of comparison. The fact that the parents of the progenies concerned were from stocks that had been selfed for from two to four generations should make the results more trustworthy than they would otherwise be. The relevant data are given in table 11.

TABLE 11

Comparison of mean grades of variegation of parents and their F_1 progeny in crosses between homozygous variegated plants.

CULTURES	GRADES OF PARENT PLANTS	MEAN GRADES OF PROGENY		
		Observed	Average	Difference
11311	1	0.82		
11312	6	4.52	2.67	
				0.58
11311-5×11312-1	1×6	3.21	3.25	
11312-1×11311-6	6×1	3.29		
17435-1×17441-2	1×6	3.85		
17441-2×17435-1	6×1	4.08	3.96	
				0.59
17435	1	1.00	3.37	
17441	6	5.75		
				0.02
17435-5×17441-7	1×6	3.35	3.35	
17441-7×17435-5	6×1	3.35		

In one of the comparisons of table 11, the F_1 ears had a mean grade of variegation almost exactly the same as the average of the mean grades of the parent cultures. In the other two comparisons, the mean grades of the progenies were somewhat, probably significantly, higher than the averages of the mean grades of the parent cultures. Since, however, one pair of parent cultures, 17435 and 17441, is involved in two of the comparisons, and since the two pairs of F_1 progenies of crosses of different individuals of these two parent cultures differ as greatly from one another as either one does from the average of the parent cultures, the data give little support to the assumption that either a high grade or a low grade variegation gene is even partially dominant to the other. If there is any tendency toward dominance, it is the higher grade variegation which shows it. This is not in agreement with EYSTER's (1928) proposed explanation to account for increased variability of the variegation gene in crosses with white.

Speculation as to how the two variegation genes act to produce the intermediate grade observed in F_1 of crosses of high grade with low grade stocks would be useless if it were not possible to undertake an investigation of the problem.

The observed results should be produced if each allelomorph influences its mate directly so that the two become approximately equal in mutability. A more plausible suggestion is that the postulated modifying genes interact to induce an approximately equal mutability of the two variegation genes intermediate between their original variabilities. If so, however, each of the two variegation genes must presumably return to its original state later when removed from the influence of its unlike mate or of the modifying factor associated with its mate, for there is marked segregation in grade of variegation in F_2 of crosses of low grade with high grade stocks. Now that the writer has found in maize collected in the Andes Mountains of South America what he had looked for in vain for many years in North America, a homozygous variegated race with red cobs, it should be possible to identify in F_2 and later generations of crosses of unlike variegated races the particular variegation genes present in any individual, just as it has been possible in the past to do this in crosses of variegated with red cobbed white races. But such a study must await the synthesis of a stock that combines with variegated pericarp and dominant red cob the closely linked recessive tassel seed 2.

There is the further possibility that the same intermediate grade of variegation in F_1 and similar segregation in F_2 of crosses of low grade by high grade variegated races might result if the low grade gene and its high

grade mate maintain their original variabilities uninfluenced by their respective allelomorphs or by any modifying genes associated with them. Thus, in a cross combining a grade 1 gene with a grade 6 one, $V_1 V_6$, if each gene mutates, or its elements assort, at its original rate, the resulting grade of variegation should be intermediate between the grades of the parent stocks, $V_1 V_1$ and $V_6 V_6$.

Certain data presented in one of the writer's earlier papers (EMERSON 1917), were interpreted as indicating that, in a cross of unlike variegated races, the two variegation genes retain their characteristic mutability. A cross of a very light variegated strain with a medium dark variegated one produced F_1 ears which were recorded as medium variegated. Thirty of these F_1 ears were pollinated by pure white races. From variegated kernels of these ears, 582 plants were grown. Their ears were divided on the basis of intensity of variegation into two approximately equal lots recorded as medium variegated and light variegated. From the same thirty parent ears, there were planted all the kernels that were self colored or partly (more than one tenth) self colored, and these produced 165 plants. The variegated ears of these plants were classified by the same standards used in classifying the ears from variegated kernels. The results are given in table 12.

TABLE 12

Percentage of self colored, medium variegated, and light variegated ears in the progeny of self colored, partly self colored, and variegated seeds of variegated ears pollinated by white races.

TYPE OF SEEDS PLANTED	PERCENTAGE OF PROGENY		
	Self colored	Medium variegated	Light variegated
Variegated	..	48.97	51.03
Less than half self colored	11.76	36.77	51.47
More than half self colored	29.63	12.96	57.41
Self colored	37.21	..	62.79

The important feature of these records is that, as the percentage of self colored ears in the progeny increased, the percentage of medium variegated ears decreased. From this it was concluded that "in these F_1 plants the factor for medium variegation mutates much more frequently than the factor for very light variegation—$V_m V_l$ ordinarily becomes (by mutation) SV_l rather than $V_m S$."

In so far as these early records can be regarded as trustworthy—in the more recent work there have not been encountered cultures which could

be classified into two sharply separated groups—they suggest that variegation genes of F_1 crosses of low grade with high grade races maintain more or less their normal mutability. But if mutation of a low grade variegation gene is not accelerated either directly by its high grade mate or by modifying genes associated with it, it is difficult to see how a white gene or its associated modifier could influence the mutability of a similar variegation gene in crosses of low grade variegation with white. The material now for the first time available should make possible a more satisfactory analysis of these problems.

SUMMARY

In this paper, which deals with the so-called "calico" type of variegated maize pericarp, it has been shown that:

1. Mutations from variegation to self color occur more frequently in the heterozygous, *VW*, than in the homozygous, *VV*, segregates from crosses of variegated, *VV*, with white, *WW*.

2. Different white races influence differently the mutability of the variegation gene in crosses of variegated with white.

3. White stocks recovered as segregates from heterozygous variegated stocks of low grade increase the mutability of the variegation gene in crosses less than do the white races tested.

4. Reciprocal crosses of variegated with white and of low with high grade variegation are not significantly different in grade.

5. Dominance of neither low grade nor high grade variegation in crosses of the two types has been demonstrated, the grade of F_1 being intermediate between the parental grades.

These facts are thought by the writer to be best interpreted by the assumption that there exist modifying genes linked with the variegation gene, which influence the mutability of the latter.

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INHERITANCE OF PUBESCENCE IN SOY BEANS AND ITS RELATION TO POD COLOR[1]

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INTRODUCTION

NAGAI and SAITO (1923) described a glabrous soy bean plant that appeared in the F_2 generation of a cross between two pubescent parent plants. The data presented showed the glabrous character to be a simple mendelian dominant to pubescence, and the factor pair was designated as P_1p_1. STEWART and WENTZ (1926) reported the discovery of a glabrous soybean outwardly resembling the type found by NAGAI and SAITO (1923), also arising from a cross between two pubescent parents, but behaving as a recessive to the pubescent type instead of as a dominant. This factor pair was designated P_2p_2.

The F_2 results reported by STEWART and WENTZ (1926) deviated quite widely from a 3:1 ratio, an actual ratio of 6.76:1 being obtained. Results of the F_3 and later generations, however, fitted a 3:1 ratio much better. On the basis of this and other considerations, the authors interpreted the inheritance as being due to a single pair of mendelian factors, and concluded that the character they studied was not the same as that described by NAGAI and SAITO (1923).

As pointed out by OWEN (1927) critical evidence on the genetic relationship of these two glabrous types should be furnished by a study of a cross between them. We propose to present in this paper the results obtained

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in a study of such a cross, a genetic interpretation of them, and the relation between pod color and the presence or absence of pubescence.

SOURCE OF PARENT MATERIAL

Several years ago, through the courtesy of Mr. W. J. MORSE of the United States Department of Agriculture, we obtained a glabrous soybean, which in crosses with pubescent types, has proved itself to be dominant. This likely carried the same factor for glabrousness that was carried by the type discovered by NAGAI and SAITO (1923). This is indicated by the fact that OWEN (1927) made use of glabrous types from both sources in crosses with pubescent types and obtained similar results, so far as the inheritance of glabrousness was concerned. Seed of the recessive glabrous type was obtained through the kindness of Professor WENTZ.

In our crossing experiments, we were successful in making a cross between the recessive glabrous type used as the female parent, and the dominant type used as the male. One pod was produced containing two seeds. The particular dominant glabrous plant used as a parent in this cross was a homozygous segregate from a cross between Medium Green and the original dominant glabrous type secured from Mr. MORSE. In addition to dominant glabrousness from one parent, it had black pods and green cotyledons from the Medium Green parent. Since the green color of the cotyledons is, in this case, maternally inherited, it does not enter into consideration.

F_1 RESULTS

The two F_1 plants were grown in the greenhouse and were glabrous.

F_2 RESULTS

Plants of the F_2 generation were grown in the field in the summer of 1928. Both glabrous and pubescent plants were produced. Of a total of 232 plants grown, 183 were glabrous and 49 were pubescent. The data seem to fit a 13:3 ratio better than a 3:1, as evidenced by the fact that the deviation divided by the probable error on a 3:1 basis was 2.02, whereas on a 13:3 basis it was only 1.37.

The 13:3 ratio would be produced in F_2 if the dominant glabrous parent is assumed to carry a factor for pubescence (P_2), but is inhibited from expressing the pubescent character by an inhibiting factor (P_1), and if the recessive glabrous parent is assumed to carry the recessive factor for pubescence (p_2) as well as the recessive inhibiting factor (p_1). The genetic constitutions of the parental, F_1, and F_2 generations, and the breeding behavior in F_3 are as follows:

Parents	F_1	F_2	*Breeding behavior in* F_3
		$1P_1P_1P_2P_2$ Glabrous	All glabrous
$P_1P_1P_2P_2$		$2P_1P_1P_2p_2$ Glabrous	All glabrous
Glabrous		$2P_1p_1P_2P_2$ Glabrous	3 glabrous: 1 pubescent
×	$P_1p_1P_2p_2$	$4P_1p_1P_2p_2$ Glabrous	13 glabrous: 3 pubescent
	Glabrous	$2P_1p_1p_2p_2$ Glabrous	All glabrous
$p_1p_1p_2p_2$		$1P_1P_1p_2p_2$ Glabrous	All glabrous
Glabrous		$1p_1p_1p_2p_2$ Glabrous	All glabrous
		$2p_1p_1P_2$ Pubescent	3 pubescent: 1 glabrous
		$1p_1p_1P_2P_2$ Pubescent	All pubescent

We should expect, therefore, that of 16 plants in the F_2 generation, there would be the following types in the following ratio based upon their breeding behavior in the F_3 generation.

	F_2 ratio	*F_3 ratio*
16	13 glabrous	7 would breed true for glabrousness
		2 would segregate, 3 glabrous: 1 pubescent
		4 would segregate, 13 glabrous: 3 pubescent
	3 pubescent	2 would segregate, 3 pubescent: 1 glabrous
		1 would breed true for pubescence

F_3 RESULTS

To test this factorial hypothesis, seeds of 158 F_2 plants were planted in sand benches in the greenhouse, as pubescent and glabrous plants can easily be distinguished in the seedling stage. Of these F_2 plants, 109 were glabrous and 49 were pubescent. The data are summarized[3] in table 1. On account of the low seed yield of the glabrous plants, the num-

TABLE 1

Classification of F_3 progeny on basis of breeding behavior with reference to the glabrous-pubescent character pair in soy beans.

TYPE OF F_2 PARENT	F_3 BREEDING BEHAVIOR	OBSERVED RESULTS	CORRECTED RESULTS	EXPECTED RATIO
Glabrous	Bred true	52	61	7
	Segregate 3:1	22	26	2
	Segregate 13:3	35	41	4
Pubescent	Segregate 3:1	36	22	2
	Bred true	13	8	1
Totals		158	158	16

$\chi_3^2 = 3.145$ $\quad P = .5358$

[3] Due to lack of space, detailed data cannot be given. The authors would be glad to furnish a typewritten copy of the tables for the inspection of anyone particularly interested in seeing them.

ber in the progeny was smaller than desirable, especially for differentiation between 3:1 and 13:3 ratios. However, deviations and probable errors were calculated for each progeny for each ratio, and each segregating progeny from a glabrous parent was classed as a 3:1 or a 13:3 according to which ratio had the smaller quotient (deviation ÷ probable error), and therefore the better fit.

Some difficulty was experienced in classifying the progeny of pubescent F_2 parents. Thirteen progenies were classed as breeding true for pubescence, and 36 as segregating in a 3:1 ratio. Of those classed as breeding true, four produced a few glabrous plants. Thus one plant produced 29 pubescent: 2 glabrous, two plants each, 49 pubescent: 1 glabrous, and the fourth, 47 pubescent: 3 glabrous. It is not certain just how these anomalous results may be accounted for. The pods were picked off the plants and shelled by hand. For this reason, it is very unlikely that the glabrous plants are the result of seed mixture. As the F_2 plants were grown close together in the row so that the branches of adjacent plants were in contact, a certain amount of natural crossing may have occurred. It is known that natural crosses take place in soybeans more or less frequently, depending upon the variety, locality, season, and probably other factors. If a pollen grain from a dominant glabrous plant fertilizes an ovule on a pubescent plant, the seed thus produced will develop into a glabrous plant. Such mixtures, due to natural crossing, can not be identified in progenies of heterozygous or homozygous dominant parents, though they probably occur with equal frequency. We believe we are justified in classing these four progenies with those breeding true for pubescence (1) because such wide deviations from a 3:1 ratio, due to chance alone, are improbable, and (2) because natural crosses are known in soybeans, and are known to have produced anomalous results in other genetic studies (WOODWORTH (1921); STEWART and WENTZ (1926)).

Since the F_2 glabrous and pubescent plants tested in F_3 were not in the ratio of 13:3, it was necessary to correct the results before determining the deviation from the expected ratio. This procedure has been followed by LINDSTROM (1917) in studies on aleurone and chlorophyll factors in corn, and by WOODWORTH (1921) in determining the genetic relation between cotyledon and seed-coat colors in soybeans. The correction is justifiable and necessary in the present instance, since the wide deviation from a 13:3 ratio in the numbers of F_2 plants tested is not due to segregation and recombination.

The low value of χ^2, and the consequent high value of P, (table 1) indicate that the above genetic hypothesis is the correct one. Hence, it appears

that the dominant type of glabrousness carried a pubescence factor (P_2) and an inhibiting factor (P_1), and the recessive type, the recessive allelomorphs of both (p_1, p_2). It should be possible to isolate, by appropriate crosses, still a third glabrous type in homozygous condition; namely, that which is recessive for the pubescence factor (p_2), but dominant for the inhibiting factor (P_1). The genetic constitutions of the three homozygous glabrous types are $P_1P_1P_2P_2$, $P_1P_1p_2p_2$, and $p_1p_1p_2p_2$.

Factor symbols P_1p_1 and P_2p_2 have been used in this case, in order to avoid revisions in symbolism respecting other character pairs in soybeans. It appears that NAGAI and SAITO (1923) in their experiments with the glabrous type, were really studying the effect of an inhibiting factor which prevented the production of hairs on the plant. Hence, P_1 is retained but thought of as an inhibitor of pubescence rather than as a factor for glabrousness. Also, STEWART and WENTZ (1926) were concerned with a single factor pair designated by them P_2p_2, the dominant member producing pubescence, the recessive member, glabrousness. The inhibiting factor was recessive and therefore not involved in their experiments. The symbol I has usually been used to designate inhibition, but in soybeans this symbol is already in use to designate inhibition of black and brown pigments in the seed-coat. Hence, it appears simplest to retain P_1p_1 and P_2p_2 to express genetically the glabrous-pubescence relationship in soybeans.

POD COLOR

The dominant glabrous type used in the cross had dark or black pods (L) and the recessive type light brown pods (l). The F_1 plants bore dark pods, and in F_2 there was segregation for pod color in approximately a 3:1 ratio. Of a total of 232 plants, 183 were dark-podded, and 50 were light-podded. This represents a deviation of 8 from expectation, with a probable error of 4.908. The quotient (deviation ÷ probable error) is 1.63. Thus, one factor pair (Ll) is involved, and the results confirm those reported elsewhere (WOODWORTH (1923)).

RELATION BETWEEN POD COLOR AND PRESENCE OR ABSENCE OF PUBESCENCE

The cross between the dominant and recessive glabrous types affords an opportunity for determining whether there is any linkage between the factor pairs Ll and P_1p_1 or Ll and P_2p_2. The data are summarized in table 2.

The actual results obtained corresponded quite closely with those expected on the basis of independence between the factor pairs concerned.

TABLE 2

Classification of F_2 plants showing independent relation between presence and absence of pubescence and pod color.

TYPES		ACTUAL NUMBERS	EXPECTED NUMBERS	EXPECTED RATIO
Pubescence	Pod Color			
Glabrous	Dark	146	141	39
	Light	37	47	13
Pubescent	Dark	36	33	9
	Light	13	11	3
Totals		232	232	64

$\chi^2 = 2.9416$ $P = .40218$

It is, therefore, concluded that the factor pair *Ll* is independent of the factor pairs P_1p_1 and P_2p_2 for the presence and absence of pubescence.

SUMMARY

1. In a cross between a dominant glabrous and a recessive glabrous soybean, the F_1 was glabrous and there was segregation in the F_2 in the ratio of 13 glabrous to 3 pubescent plants. The F_2 ratio was substantiated by the F_3 results.

2. The data were interpreted as being the result of the interaction of two factor pairs P_1p_1 and P_2p_2. P_2 is responsible for pubescence; p_2 for glabrousness; P_1 inhibits P_2 from producing pubescence, thus causing glabrousness; p_1 has no effect on P_2. Thus three different pure types of glabrous plants are possible, namely, $P_1P_1P_2P_2$, $P_1P_1p_2p_2$, and $p_1p_1p_2p_2$. The pure pubescent type is $p_1p_1P_2P_2$.

3. In F_2 two color types of pods were found, dark (*L*) and light (*l*). Segregation occurred in the ratio of 3 dark to 1 light.

4. The presence or absence of pubescence was found to be inherited independently of pod color.

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